植 物 分 类 学 报
5卷 4期 1956年11月

馬先蒿屬的一个新系統(二續)

鍾 补 求

(中国科学院植物研究所)

馬先蒿的原始中心(續)

依据上面所說的理由，我們已經完全与泊蘭氏的意見一样地达到了一个結論，以为馬先蒿的原始中心是在环極省区之內。但是，包括在一个以夏季等温度 15°C 为界的圈子里的是一个广大的面积，一个广大到使人沒有精确感的面积。所以我們一定要設法来看一下，是否有可能把这一个大面积縮到一个較小的面积里，这样，因为它的紧湊，可以給我們以一个比較确切的概念。

为了这样一个目的，对于所有古老种类[1]的分布加以一个更为严密的檢查，就成为必要了，因为只有这些領先的群的祖先，才能对于这一問題發生一些闡明的作用。合乎这一要求的，只有五个在北極地区的种类，可以加以考慮。这些是被認为各群的創始种的种类，如：Rhizophyllum 群的 *P. flammea* L.，Sceptrum 群的 *P. capitata* Adams，Apocladus 群的 *P. hirsuta* L. 和 *P. lanata* Cham. et Schl.，以及 Cladomania 群的 *P. Langsdorffii* Fisch.。在設法更正确地找出这些种类的分布区域时，我發現了荷尔登氏[2]，以他的精彩的工作，在一些种类中成为我的論据了。为了方便起見，也許还是不管重要性的次序，而先从他那里引来三种的地理分布为較好：

1) 为了使我們对于我們辯論所根据的基础得到更坚实的可靠性，这是合理的来在这里再返回一下我們在形态和亲緣部份中所作的討論。在那里，我們曾經达到了一个無可爭辯的結果，关于 Rhizophyllum 群的前进的花的大小和 Sceptrum 群中下唇的長短和位置的連續的發展阶段。以 *P. flammea* L. 的很小的花为根据，这似乎是很不可能在 Rhizophyllum群中，曾經存在过比这一种更为原始的种类了。同样地，看到了 *P. capitata* Adams 的下唇的很合攏的位置以及它的短度，这也許是沒有什么危險，来猜想在 Sceptrum 中，也从沒有过比这更为古老的种类。更有加者，按着 *P. flammea* L.、*P. Oederi* Vahl、*P. pseudoversicolor* H.-M.、*P. hobachanensis* Bonati、*P. rhynchodonta* Franch.、*P. filicula* Franch.、*P. robusta* Hk. f.、*P. bella* Hk. f.、*P. longiflora* Rudolph 和 *P. megalantha* Don 等种类的前后的次字，我們似乎可以确知 Rhizophyllum 的亲緣綫上，并沒有間断的痕迹；同样按照 *P. capitata* Adams、*P. Sceptrum-carolinum* L.、*P. tristis* L.、*P. galeata* Bonati、*P. dolichocymba* H.-M.、*P. trichoglossa* Hk. f.、*P. Vialii* Franch. 等等的順字，Sceptrum 群的世代鏈系是有理由被認为連續而沒有失落的环节的。

2) 荷尔登，E.：阿拉斯加及育空的植物志，IX (1949)，馬先蒿羼，頁 1401—1420。

1. *P. capitata* Adams：亚洲：自叶尼塞河向东，經泰米尔地域复沿海岸至初克啓半島，南至潘西那，堪察加南部和帕拉姆西島。美洲：自阿拉斯加和育空經維多利亞地域，美尔維尔島和爱莱斯美地域至南巴飞因地域，南向至英屬哥倫比亞东南部的山上（頁1403）

2. *P. lanata* Cham. et Schl.：欧洲：斯彼兹柏尔根，諾佛耶齐姆利亞，維戛曲，北烏拉尔。亞洲：从烏拉尔至初克啓半島，在叶尼塞南至北緯59度左右，再至耶柯次克地区及千島群島北部（帕拉姆西島），也在准噶尔阿拉道山中孤存（按照克利罗夫报道）。美洲：自阿拉斯加和育空經班克斯地域，南至却罗脫皇后島，英屬哥倫比亞南部，哈德孙海灣北部以及拉不拉多半島的西北部，以至格陵蘭西北部（頁1408）。

3. *P. Langsdorffii* Fisch.：亞洲：自泰米尔至灤歧尔島，海雷尔島及初克啓半島，南至卡拉金斯克島。美洲：阿拉斯加和育空經班克斯地域及爱莱斯美地域至巴飞因地域，南至北極海岸，格陵蘭西北部（頁1409）。

現在再来看一下其余兩种——*P. flammea* L. 和 *P. hirsuta* L.——的分布区域。前一种的面积，照林泊利許氏所报导，包括加拿大北部的一部份（北部落基山及以北地区），拉不拉多，格陵蘭，冰島及拉普蘭德；后一种是拉不拉多，巴飞因地域，爱莱斯美地域，斯彼兹柏尔根，拉普蘭德，諾佛耶齐姆利亞，再沿叶尼塞、泰米尔、俄雷內克及利那諸河流域分布。

在上面，除了 *P. lanata* Cham. et Schl. 因它的分布几乎遍布北極而不能給我們以一些特殊的啓示外，所有其余的种类，因为在它們分布上有些相同点和异致点，似乎給我們以一些有意思的事迹。*P. capitata* Adams 和 *P. Langsdorffii* Fisch. 可以看到遍布于美洲北極，連續西向而各自达到極北的西伯利亞的叶尼塞与泰米尔地区，但是却未見于極北的西部西伯利亞和北極欧洲。这里可以注意的是它們兩者，都以格陵蘭为其分布区的最东据点。至于其他兩种，*P. flammea* L. 和 *P. hirsuta* L.，它們的面积在它們之間仅有些少的区别，但同上面兩种比較，則大不相同。在新世界，虽然面积有些大小，却都占着北極美洲的一部份；在旧世界，前者的面积，主要产于拉普蘭德，而后一种呢，則向东伸展至利那河地区。它們是不存在于北極的西伯利亞东部和北極的北美西部（至少是不見于阿拉斯加和育空）。这里最有趣的一点是，不管它們的分布面积如何不同，这5种却都在格陵蘭的植物区系內存在。現在我們要借此机会来提醒一下我們的讀者，关于我們在本文第一部份中所提到的本屬系二元發生的假設——一个假設，要求那兩个代表群：Rhizophyllum 和 Sceptrum 的古老类型之在同一地区發生而且同时存在，以至它們之間的以后發生杂交，因而生長某些新成的，但是仍然是原始的类

型来，而再由这些类型，生出派生的群来。現在看来，格陵蘭似乎正是那个能够合乎这个要求的唯一地方，因为那無疑是很难于把所有这些原始类型集中于这一島上的事实，看做完全是偶然巧合的。我想很少人会反对我把这5种当作那四个先进群的各自的祖先的見解的，虽然有些人也許会不很願意相信那后面的3种是由于杂交而發生的。現在似乎很明显了，这些原始种类的分布的更精确的檢查，巳經給与我們一个答案，說明本屬的确切的原始中心是在格陵蘭了。为了給我的意見以一个更清晰的观念，我們可以把这些种类的分布面积中之地址的安排，改換一下，成为更易了解的次序如下：

1. *P. flammea* L.：自格陵蘭向西至拉不拉多和加拿大的落基山；向东，經由冰島至拉普蘭德。

2. *P. capitata* Adams：自格陵蘭向西至爱莱斯美地域，南向至巴飞因地域；自爱莱斯美地域向西南，經美尔維尔島、維多利亞地域至大熊湖，从这里，一条路綫引向南方至英屬哥倫比亞东南部，另一条路綫向西至育空和阿拉斯加，越过海峽至初克啓半島，自此，分布路綫一直引向叶尼塞河流域。

3. *P. hirsuta* L.：自格陵蘭西向至爱莱斯美地域，南向至巴非因地域与拉不拉多；自格林蘭东至斯彼兹柏尔根与拉普蘭德，前一綫經諾佛耶齐姆利亞而至西伯利亞而后一綫直向东伸展，兩者在叶尼塞会合；从此經泰米尔与俄雷內克流域，以終止于利那河流域。

4. *P. lanata* Cham. et Schl.：从格陵蘭向南至拉不拉多和北哈德孙海灣，西北至班克斯地域，向西至育空，轉向南方，分布綫来至却罗脫皇后島和英屬哥倫比亞南部；自育空向西，它来到阿拉斯加；自格陵蘭东向，它經由斯彼兹柏尔根、諾佛耶齐姆利亞和維戛曲而达于北烏拉尔；再东向，路綫又伸展过叶尼塞流域而达于耶柯次克，以終止于千島群島[1]。

5. *P. Langsdorffii* Fisch.：自格陵蘭至爱萊斯美地域，南向至巴非因地域，西南至班克斯地域，再南至育空，折向西經由阿拉斯加；在越至初克啓半島后，一綫向西南至卡拉金斯克島，另一綫向西北至灤歧尔島及海雷尔島，其主綫則直达泰米尔地域。

如上所述，这是十分明显的，如果以格陵蘭为本屬的确切的分布中心，那末將得到一个与亲緣發展保持着密切一致的分布款式。当然，紧随着这样的一个說法，將是这些种类是怎样地来到格陵蘭的問題，因为十分显然，它們的分布是与这个島的現在地文情

1) *P. lanata* Cham. et Schl. 的分布路綫，在东西伯利亚分明是导向东南而不是直向东方以至安那提尔，所以兩条——从格陵蘭向东和向西——路綫并不在白令海峽相遇。这也給我們以一个观念，来想这一种也是在这个島上出生的。

形不相配合的。对于这，我們还要再說一些話，不过是在很不同的題目下来說了。

（三） 馬先蒿的紀年表

在究問到馬先蒿年表的时候，將有兩个重要点要闡明，那就是：本屬自己的古老性，和各个它所包含的大分类單位的紀年次序。

講到本屬的古老性，林泊利許氏（頁 161）曾經提出过：以为是在白堊紀的末期或者始新紀的初期出生的。泊蘭氏虽然沒有肯定地表明，似乎意指着一个晚得很多的时代，因为他在地理分布方面的論述，主要涉及冰期时代。要証明这样的設想的古老性，比較直接而可靠的論断必須向古生物学的資料中去寻找，可是在这一方面，馬先蒿是缺乏化石記录的[1]。在这样的条件下，想得到本屬的年齡的概念，唯一的方法是由以現有分布中的特点来与所知在已往地質年代中所發生过的大陆輪廓的緩慢变迁相比較，来得到一些間接的論断了。現在我們已經知道本屬的确切的分布中心是在格陵蘭，我們，以这个島現在所占的特殊地文位置，可以好好地利用它一下。我們將再来問一下这些种类是怎样来在这島上生存的。

在这样的一个問題前面，那必須先来决定到底在格陵蘭及其他島嶼如冰島和斯彼兹柏尔根等的植物区系中的馬先蒿以及其他植物是否屬于外来性質的，即由大陆上迁移入境的呢？由这一問題便要介紹进另一个有趣的，关于冰川对于这些島上植被的作用的問題来了。馬修[2]，在他的"第三紀中大陆的想像的輪廓"一文，在洪积期部份中，談到了这一問題。他在那里說，可能格陵蘭的冰川是这样的广漠，以至于一直超越了这个島的陆地的四緣，所以以它的一扫而空的勢力，把冰期前所有任何生命，全部毁灭。如果这一論断是合乎事实的話，那末我們一定要認为这些馬先蒿不是本島的土著植物区系的一部份，而是冰期后的迁入者了。讓我們来看一下事实如何。我怀疑有人会相信种子会从东面越过横在欧洲大陆与格陵蘭之間的大海而来到島上。当然，我們也要把种子的偶然間的分布計算在內，但是这在一种或甚至極少数的种类的情形下或許可能，但是不很可能多到像現在存在于以为系代替了为冰的作用所完全毁灭了的一个植物区系的現代的植被中的 7 种馬先蒿那样多。所以在一个屬里有这样多的种类的分布，它的唯一的机会，就只有从西而来，那就是从北美而来。但是十分清楚，分布的特点却不允許这样一个簡單的解說，那是因为它需要一个几乎不容置信的忆說来解答它。以 2 种

1) 參照林泊利許氏所提到的（前書 161 頁）关于泊克斯氏"兩極的植物地理"（柏林，1918）28 頁中所說的唯一的馬先蒿 *P. sylvatica* 的記录。

2) 此文發表于美国自然历史博物館彙报 22 卷（1906），頁 353—383。所有地圖，又为巴宰考克氏所轉載。

P. flammea L. 和 *P. hirsuta* L. 为例吧。如果它們是被当作在欧洲發生的，那末，西面被大海所擋，它們在东部北極美洲連格陵蘭在內的存在，就只能解釋为由欧洲东向分布的了。但是，我們又怎样地来解釋它們在北極西伯利亞的东部和北極美洲的西部的不存在呢？世界上还沒有知道有一种原因，有这样大的力量，能在这样广漠的地区內把植物种类的数量完全消灭而不留一些遺迹，即使是冰川的力量。就使冰川有能力实現这样的奇迹，仍然我們的古地理智識，不允許这样一个忆說，因为亞洲在第四紀中是各洲中比較最少受到冰害的洲。如果以为先在美洲發生，那末它們在拉普蘭德和斯堪的納維亞的分布，还是存在着同样的解釋的困难。

現在这里有一个林泊利許氏所持的与此正相反的見解，他在 162 頁中表白如："因为冰島在安齐路斯时期被認为有着一个較暖的天气，那时的北部海岸比現时的西海岸还要暖，同样地，斯彼茲柏尔根在冰期后的年代里，有着一个比現在还要溫和的气候。斯彼茲柏尔根也許是沒有冰的，由此就可以解釋这些所說的种类，是在格陵蘭和斯彼茲柏尔根上渡过了冰期的。"对我来說，这是对于在这些島上分布着的馬先蒿种类的一个十分可以贊許的答案[1)]，因为它解决了一个問題，就是今日在島上仍存留的植物，乃是冰期以前在那里的一些种类的后代，虽然它还沒有能够对于这些种类怎样来在格陵蘭的問題加以完滿的解說，因为在东面，大海成为它們分布的一个無法逾越的障碍，而在西面呢，在它們各自的分布領域內，存在着一些沒有这些种类的大片土地，使得由西向东分布的解釋，似乎有些难以接受。如果它們在格陵蘭的存在旣不能归于由欧洲向西分布，也不能归于由北美向东分布，那末我們將怎样来得到一个答案呢？

生物学家差不多一致相信格陵蘭和一些較小的島嶼，以及北美和欧洲从前在地質年代里，曾經是一个大陆塊的北部的一部份。这一个設想的大陆塊，对于前面所提的問題，給与一个合宜的答案。以它們的現时分布所啓示給我們的看来，很明显，事实上这些种类从来也沒有迁居到格陵蘭去过，而正相反，它們是从格陵蘭，这个生出它們来的地方，迁居到世界的其他地区。并不是沒有可能，它們当格陵蘭脫离大陆的时候，已然有了自己的分布面积，而那些面积無論如何已然超过了那时在那个陆塊上把格陵蘭自其他部份划分开来的那个想像的界綫了。

事情似乎有些开朗了。現在如果我們能够知道那个陆塊北部在什么年代里分裂的話，对于計算一个本屬的約略的古老性，是不会离得太远的了。可惜，事情却并不如此

1) 参閱戈德同書 224 頁，与"自然科学百年来的进步" 758 頁，植物地理部份(1955)。也可以参看雷德，C.：現在英倫島上植物的数量与冰期的关系一文，載：植物生态杂志，1913，42—46 頁。在那里，他也承認了一些北極——高山种类的生渡冰期于英倫島上的事实(43 頁，第 6 段)。

簡單,因为对于这个分裂的日子,人們曾經表示过不同的意見。这一問題現在已經变成了一个相互的問題了,在这里面,我們的問題的合理解决,可以对于兩个相反意見的贊成或反对方面,提供更多的証据。

馬修在上面所提到的文章內,把这个日期定在第三紀开始的时候。到了始新世,他說,海的漲淹又使陆洲和島嶼为水所隔离。虽然他承認在漸新世[1]曾于北美和欧洲間又有过交通而哺乳类动物曾来往迁移,但这被認为幷非由于格陵蘭的居間而發生的直接接触,而是經由"白令地峽"而实現的(頁 363 与 365)。在这个島嶼与欧洲大陆之間的深海,使得兩者在分离后不再重新接合,但是格陵蘭的西部,被視为曾在中新世又与北美大陆發生了一个时期的接触。

与上面的說法正相反的,我們可以回忆林泊利許氏曾在他的地理分布部份的論述中,涉及阿尔特脫氏的提議,一方面經斯彼茲柏尔根格陵蘭与斯堪的納維亞之間,另一方面經冰島格陵蘭与西欧之間,在洪积世中的相互联系[2]。当然,林氏仅仅用这一見解来解釋一些馬先蒿在格陵蘭的存在問題,这是因为他把 *P. Artselaeri* Maxim.[3] 当作系在視为本屬搖籃的阿尔泰天山山脉中最先發生的古老种类的緣故,所以引导他入于一个錯誤的观念,以为格陵蘭所有的种类,都是由外面世界上移入的。

現在这就变成了一个最有趣味的問題,来决定在这兩个——白堊紀(或者早期始新世)或者更新世——远隔的地質年代之中,那一个应被作为正像我們現在所見的格陵蘭完全分离的情形的比較适合而有理的时期呢?而这时期又是这样密切地关連着馬先蒿的古老性的問題。

讓我們先来假定像馬修氏所認为格陵蘭是在第三紀开始的时候从大陆分离的吧。就因为它帶了所有最古老的馬先蒿种类而离开的这一事实,我們就不得不承認这些种类的發生,無論如何是先于这个島嶼的分离,而始新世的早期或者白堊紀的末期就必須被接受来作为本屬年齡的一个时期,正像上面已經指出的一般,是与林泊利許氏的提議相合的。但是为了下面所指出的理由,对于我說来,在馬先蒿分布的观点上看来,是一个十分太早的时期。

---

1) 在地質学名詞中,Eocene 的譯义是"始新世;始新統",在 Oligocene 后,則是"漸新統(世)",而在 Miocene 后是"中新統,中新世",Pleiocene 与 Pleistocene 里,則又分別作"上新世(統)"和"更新世(統)"。因为名詞的不統一,我这里只能用最常見的"世"了。

2) Arldt, T.: 古地理学手册, I (1919),頁 591。

3) 如果因为它們的無莖的体态,*P. Artselaeri* Maxim. 和 *P. acaulis* Wulf 被視为本屬發韌的类型,像 Limpricht 所为的那样,那末,給一个像这样的具有远距离的,間断分布面积的二同型的种类,是由什么源流而来的問題,以一正确答复的要求,無疑地將会給那位著作者以很大的困难的;而他,却未曾注意到給这一重要的問題以一个滿意的回答。

从遺留的化石中，我們知道了在白堊紀的时候，格陵蘭的气候是很暖的，这样地暖因而它的植物区系的成份中，有很濃厚的暖温帶色彩[1]。在地形上說来，这个島上是沒有强烈的起伏的。这是十分难于了解为什么在很低的高度和很温和的气候相結合的情况下所生出来的植物种类，能够渡过冰川作用而終于变为北極——高山的成分了呢？

我們由形态和亲緣方面的研究而知道了馬先蒿屬各群和亞群中的遺傳綫沒有什么中断的标志，而同时，最保守的和最前进的类型的共存，而在兩極端之間又沒有丢失的环节这一事实，也告訴了我們在馬先蒿一屬內，种的絕灭，是很少見到的。所以，这是难于想像的，經过了漫長的地質年代，进化的鉸鏈能够这样完整地保持着原样，而并沒有因为气候的变迁和其他自然条件的关系，而在它們的持續中感受到一些損缺。

再讓我們从种的稳定性的观点上来看一下这一事情。在生物学的領域中，大家都熟知，孤存在生物的变化中，和在种的形成中，起着一个很重要的作用。現在如果在格陵蘭的馬先蒿种类，一直从始新世的初期这个島从大陆分离的时候，一直就孤存到現在，那末，我們將怎样来解釋这种現象，就是被隔离了这样久，它們，像在同一种类的在島上的和在大陆上的群体相比較之下所显示的一般，完全保留在稳定的情形下而沒有感到一絲一毫的孤存的影响呢？

其他还有在这个島上存在着一个構造得很精巧而具長嘴的类型 *P. groenlandica* Retz. 这样的一个疑难問題。事实上，成問題的倒不是它为什么在那里，而是它迁移到島上来的时候發生問題。这几乎是沒有疑問的，这一种出生在加里福尼亞或更南地区，所以格陵蘭是在它的原始中心的同一經向分布綫上。一定是有一个沿經綫的迁移把它帶到这島上来，这一迁移可能在以后的时期里，当格陵蘭在分离后又与北美联合的时候，也可能当格陵蘭与美洲結合的时期的后一段时間內。我們还記得馬修氏的提議，关于这样的一个在中新世發生的重新联合的說法。如所周知，中新世，尤其是后半段，是一个标志着在北極地区天气漸漸变坏的时期。植物的迁移，如果一般的信念是正确的話，应該在那时候开始它的南向的潮流，而我們看不出为什么 *P. groenlandica* Retz. 單独地把它的迁移，逆着一般的潮流而指向北方呢？

現在可以看一看如果第四紀被当作格陵蘭与大陆脫离的时間，事情將要怎样呢？在接受了这一建議之后，一个完全不同的展望就会出現了；上面所指出的每一个对馬修氏的假定發生爭論的論点，都將反过来拥护后面一个見解了。当然，这是既沒有必要也沒有理由来設想格陵蘭从大陆脫离的日期，尤其是从欧洲脫离的日期，是与本屬的出生的时間同时的或者靠近的。很可能，而且我相信这是事实，馬先蒿最先作为一个屬出現

---

1) 参閱 A. R. 华萊士: 島嶼生命(1881)，116 与 173 頁；戈德，前書頁 268；吳尔夫，前書頁 150。

的时候要比这个島的孤立早得多；也許当位置的移动来到的时候，那些古老的类型，甚至于有一些它們的較进步的后代已經有了相当大的分布面积。但是虽然如此，本屬的开端日期却是最早也不可能超过中新世的末期。如果它的古老性不被推断到遙远的白堊紀去而是放在比較現实的中新世或者上新世，这当然是比較容易使人相信为什么馬先蒿的亲緣系統是这样地完善地被保留到今天。同样地，它也將对在有机体中的孤存所發生的影响的問題，供給一个比較滿意的答案。不但因为第三紀的后期在地質年份中要更近得多，而且也因为將要到来和跟着發生的冰川活动所形成的生活条件范圍的狹縮，可能發生着一种制动器的作用来制止有机生命中变异的趋势，因而使这些种类在格陵蘭的群体，極度地保持稳定而与大陆上的完全一致。同时，这也显得更合罗輯，这些种类曾在漸漸冰化的气候中出生，所以能在以后更新世中渡过严酷的冰川作用。

最后，这里还留存着本屬中存在着賦性很不同的群以及在北極圈內有着 *P. groenlandica* Retz. 和其他"温暖"种类的問題。如果我們認为进化和分布的主要部份，是在更新世完成的話，那末冰期的活动和本屬的繁荣，一定有着密切的联系。关于冰河期，我們有"往返迁居論"的假說，最先由福孛斯所提倡，后来又为达尔文[1]所推敲而更为泊蘭氏特别結合了馬先蒿屬而加以总結与討論。这一个假設的基本观念，是建筑于在較短促的更新世中所曾数度發生过的气候变好变坏的現象上的。这个假設供給了对这兩个問題基本上可以被接受的答案。因为它的習慣地擇取北極——高山的环境，*Rhizophyllum* 就很有理由被猜想它的出生是当極高的緯度上气候已經相当变坏了的时候实現的，而 *Cladomania* 的喜好温暖的天气，可能是因为它的發生，至少它的某些較早的类型，是在一个时間里，标志着某一个或其他的間冰期的温和气候的返回，在那时候，据所知天气曾經十分暖和过，甚至于比現时所感到的还要暖和得多。这个假設也解釋了那些种类像 *P. groenlandica* Retz.、*P. verticillata* L.、*P. chamissonis* Stev. 等等存在于北極地区的緣故。像泊蘭氏所指出的它們是伴随着后退的北極——高山植物群在它們的北向迁移中同行的說法，是很少再有爭辯的可能的。

如上所述，这是显然的，作为馬先蒿的年龄，中新世的后期或者上新世，在生物地理的眼光中看来，是一个远較白堊紀或始新世为人所拥护的推断，因为它是与本屬的所有分布特点相符合的。

現在只給我們剩下了第二个問題，那就是本屬中較重要的次級分类單位的紀年次序了。在这一点中所引人注意的是許多群和亚群的复杂的年表，在这里面显示了它們的發生，既不按照它們的亲緣关系，尤其在对叶群中，而它們的后来的發展，也并沒有依照

1） 見泊蘭氏前書頁 40，附注。

相互关系的正常次序来进行。

关于各个互叶群的發生时間，似乎还看不到什么重大的次序的錯乱，但是在以后的發展上，情形就大不相同了。如果按照它們的正常次序，那末应該按着 Rhizophyllum、Sceptrum、Apocladus、Cladomania 和 Dolichomiscus 排列。但是事实上，由于某些我們一会要談及的可以想見的理由，派生的群 Cladomania 和 Apocladus 却行占先，而較它們的亲本群 Rhizophyllum 与 Sceptrum 更早地生产出进化上較高的种类，而且在較早的时日里取得了种类数目上的优势。循着这些互叶群里的發展步調的显然的次序錯乱，这同样的情形就被帶到了那些对叶群中，而且达到了一个更高的程度。这里不是 Rhizophyllum 和 Sceptrum 的最亲密的派生群 Dolichophyllum 和 Cyclocladus，如像所能合理地想望的那样，而是在亲緣上較远的 Orthosiphyonia 和 Sigmantha 兩群，最早發生而且最快前进。这些錯乱的情况，正像其他事情一样，是清晰地書写在分布的款式之中。

現在，讓我們来檢查一下那兩个領先的群，在它們的进化和迁移方面的行徑吧。在 Rhizophyllum 中，最主要的分子，是那个从 *P. flammea* L. 中分化出来，而曾經执行了本群的眞正繁育者的任务的 *P. Oederi* Vahl。在把它和它的先輩(*P. flammea* L.)在北極圈內的分布比較之后，發現了它是由后者在欧洲的群体中得来，因为它的不見于格陵蘭和北極美洲东部的事实，有效地阻止了它是在欧洲以外地区發生的一种錯誤观念的形成。我相信讀者还很記得这样一个事实，那就是它在欧洲，又由此东向，經全部西伯利亞而后南向至中国西南部——人們找到它的进化活动开始而生出盔尖有角及双齿的类型(*P. pseudoversicolor* H.-M. 和 *P. habachanensis* Bonati)的地方——的迁移所化的漫長的时間里，这一种在进化上是保持着長期的不活动性的。这是很易于了解的，在亞洲缺少十分剧烈的气候变化，这在欧美兩洲曾經对植物迁移起过推动作用，在这里使种类分布的步伐，相当展緩。

关于 Sceptrum，那最先来的 *P. capitata* Adams 正像 Rhizophyllum 中的 *P. flammea* L. 一样，在进化上是不活躍的。由它的緯綫分布把它从格陵蘭帶过了白令地峽的陆桥西向进入亞洲后，在西伯利亞的某一处产生了 *P. Sceptrum-carolinum* L.。要不是有这一个在 Sceptrum 群里的 P. Oederi Vahl 的对手种类，这一群的分布面積，可能会局限在北極地区的。但是也正像它的对手一样，它也一定曾經化了很長很長的时間向南向西迁移，而它的蹣跚来迟的进化，也同样地發現于中国西北部，在那里那个舟形盔部的 *P. rudis* Maxim. 的首次出現，記录了本群中进化类型的开端。在那兩个最老的群里对于进化步驟的迟迟行动，形成了它們的进化类型在現时都限制在較低緯度

上的特殊分布現象。

鮮明的对比，可以在 Cladomania 和 Apocladus 进化中找到。我們先来看一看前一群中的情形是怎样的。我們知道在上面已然談到的住在格陵蘭的种类，实际上并不包括这个島上所有的种类。那里还有兩种，就是 *P. labradorica* Wirsing 和 *P. lapponica* L.。这兩种不象 *P. groenlandica* Retz. 一样，它們有着緯向分布，各自地类似 *P. Ladgsdorffii* Fisch. 和 *P. lanata* Cham. et Schl.。这兩种的分布款式，与其他原始种类的相似，是一个确实的記号，表示它們是格陵蘭的土著而不像 *P. groenlandica* Retz. 系外来的迁居者。因为 *P. labradorica* Wirsing 几乎無疑地是 *P. Langsdorffii* Fisch. 的一个双齿型的后代[1]，而 *P. lapponica* L. 轉过来又是 *P. labradorica* Wirsing 的有嘴的后輩，所以同时屬于 Cladomania 群，这就揭示給我們以在这个派生群和它的亲本之間相对的發展次序中的隐藏着的关系，那就是，当格陵蘭从大陆上分离的时候，作为一个次成的群，它已經进入到双齿和有嘴的类型了。而 Rhizophyllum 和 Sceptrum 却逗留直到很后的年代里，还在最原始的"無齿型"的阶段上。这种加速的行动，說明了在各洲中的 Palustres 和 Racemosae 系广闊的分布区，以及一些种类，像 *P. numudica* Pomel 的在阿尔及利亞与 *P. zeylonica* Benth. 和 *P. Perrottetii* Benth. 的各自地在錫蘭島与尼尔歧利山中存在的緣故。

在相类似的情形下的是 Apocladus 群，包括着 Eu-apocladus 和 Pseudapocladus 兩个亞群。有着那些双齿的 *P. comosa* L. 和 *P. sudetica* Willd. 等种类广布在最高的緯度上，这兩个亞群在进化上也必然早于那兩个領先的群。Dolichomiscus 群分明是更比 Apocladus 为晚，因为成对的种 *P. acaulis* Wulf 和 *P. Artselaeri* Maxim. 是都从 *P. Sceptrum-carolinum* L. 产生出来的；这是同一个种的在欧洲和亚洲的群体生出它們来的。在这兩洲中，它們也同样地占着較南的分布区。

从互叶群中傳下来的这种显明的进化上的混乱，使得它們的对叶派生群的年表發生更大的紊乱，原因是除了影响了它們的进化之外，更重要的是进而影响了它們的出生的次序。当处于它們的正常的前后上，那些最与 Rhizophyllum 和 Sceptrum 相亲的如 Dolichophyllum, Brachyphyllum 与 Cyclocladus 应該处于对叶群队伍行列的前面，但是沒有比这距离事实更远的了。如果現时的分布款式的确有些道理的話，那末却是比較疏远的 Sigmantha 和 Orthosiphonia 現在是对叶群編队中的先鋒，因为它們是在对叶的范圍內可以在北極圈中找到种类的唯一的群了。

---

1) 讀者們可以回忆这一事实，就是 *P. Langsdorffii* Fisch. 本身，后来也有了一个双齿型的变种，那就是 var. *hians* (Eastw.) Tsoong.

在比較近代的对叶群中，可以說有着較長历史的唯一的群应該是 Eucyclocladus 了，它的分布区現在已經有一个單独的种 *P. gracilis* Wall. (subsp. stricta Tsoong) 扩展到喜馬拉雅的全長了。那些局限于中国西南部和喜馬拉雅的其他的群与亚群，很好地显示出它們出生較晚，而这也包括 Dolichophyllum 和 Brachyphyllum，那兩个最与 Rhizophyllum 相靠近的單位。

总如上述，在馬先蒿的地理分布中，似乎存在着某些問題，但当連合起来成一整体的时候，几乎可以算作一种"規律"了，而这一規律就表現在本屬的老群的緩慢但却是稳定的进化和迁移中。在次成性質的群和亚群中的驟然而却有些不規律的勃兴的进化和迁移中，这又可以返回到最高的緯度去的种类来作标志，而最后，这一規律又表現于那些限生于本屬分布面積南部的一些进化很快的[1]，現代的單位中。

至于这些現象發生的原因，似乎同时牽涉到內在的和外在的因素，也可能它們之間互起着密切的作用。在本屬發軔的兩个群中，这种古老的，純系的單位也許因为伴随而来的固有保守性，需要高于寻常的刺激——一种北極地区的比較單調的环境所不能供給的异常的刺激——使它們的正常进化作用推迟到达到了他們各自在較南緯度上的理想家园之后才来进行。至于这些疑系杂交而来的次成單位，其作用的加速，在我想来是应該归到由远緣杂交而来的杂交优势上去。这种进化的及时性，供給了这些群以众多而异样的类型，这些类型，靠着像这样的群中常常伴随着的前进性，很快地就被傳得又远又广地到大得很多的面積上去，而这是在比先輩群短得很多的时間內达成了的。

我們是否能从上面所揭露的复杂的，几乎是使人迷惘的馬先蒿年表中得到一些教益呢？它告訴了我們年表虽然几乎是地理分布中的一个不可分割的部份，却是一个非在完全而精确地掌握了形态、亲緣和分布方面的知識后，才能达到的一个目的。当然，形态供給亲緣关系以研究基础，轉过来，亲緣关系又引我們到地理分布的正确的观念中去。年表，可是一个比較复杂的問題，沒有这三方面来的深入的見地是簡直不可想像的。作为一个有趣的例子，我們举出 *P. Perrottetii* Benth.，一个似乎系本屬中的反常的，具有最長的管子而却配有無齿的盔的种类，同时也是 Cladomania 群中的唯一長管种类。这是几乎無疑的，長管这一特征是一种繼承，肯定地可以一直追踪到 Rhizophyllum 純系中發展这同一特征的 Longiflorae 和 Megalanthae 等系去。但是，拿 Cladomania 的分布事实，就是双齿的类型如 *P. Langsdorffii* Fisch. var. *hians* Tsoong、*P. labra-*

1) 进化很快是指的有些在显然較短的时間里，达到了进化的頂極而具有相当完备的进化阶段的群和亚群，这是从代表每一进化阶段的种类，缺少或仅有少数伴随着的分化类型这一事实中看出来的，如像 *Polyschistophyllum* 和 *Cyathophora* 兩群所代表的一般。

dorica Wirsing 以及有嘴类型像 *P. lapponica* L. 和 *P. resupinata* L. 等在最高緯度上的很早的出生，来和 Rhizophyllum 的双齿型 Pseudo-Oederianae 在低緯度的迟迟發生比較之后，这就大有可能，*P. Perrottetii* Benth. 要比 *P. longiflora* Rudolph 和它的近亲出生得早，而且这也不是完全不可能的，它甚至于要比 Rhizophyllum 純系中的唯一双齿的 *P. habachanensis* Bonati 都出現得早。同样地，Pseudapocladus 群中 Surrectae 系里的那些种类的最精致的花冠構造的来源，是可以跟寻到 Sceptrum 群中的 Excelsae 系去的。但是，*P. groenlandica* Retz. 現在可以在格陵蘭找到，而 *P. Vialii* Franch.，和 *P. excelsa* Hk. f. 則限生于喜馬拉雅——云南省区中。很少人將会怀疑，按照它們各自的地理分布面看来，Excelsae[1]在形态观点上虽是比 Surrectae 系为老的一个系，然而按紀年上說来，却是一个比較年青的單位。这里，在像一个屬这样低的分类單位里面的各群間的紀年关系中所表示出来的困惑情形，是能够給我們以足够的暗示，怎样的一种复杂情形我們將会在較高的分类水平像被子植物中的許多科間找到。必然地，在对于一些在形态特征上可以分屬于同等进化程度的科的古老性与进化的次序，加以深究后，將会得到远越一般想像与理解的結果的。

（四） 对于泊蘭氏經向分布綫路的投射綫路的意見

泊蘭氏在提出他的經向分布綫路的时候，作如下的理論（頁 45）：

“由特产种百分比而論，構造[2]直接証实了关于日本、美洲和欧洲的經向分布綫的証据，而特产种百分比，对于西伯利亞經向分布綫的証据，虽然奇怪地与上述的相反，但同样地也完全証实了；因为沿着其他三条經向綫，原始型花冠的百分比向着它們的赤道的界限漸漸地降低，而沿着西伯利亞經向綫，百分比却反而增高了。这种特殊的安排，一方面有力地証实了已經存在的定論，就是高加索系西伯利亞經向綫的延伸，而另一方面，使得認为中国种类的經向分布綫，系由西伯利亞而来，或喜馬拉雅經向綫，系由高加索而来，成为不可能。同时，还有直接的証据証明日本經向綫投向中国而由此以至喜馬拉雅。”

关于他的以双齿型为原始的錯誤見解，就是使得西伯利亞——土耳其斯坦省区的原始种类百分比得到不实在的增加的緣故，这一点我們現在已經明白了。不过即使这些百分比像它們应該的那样地是准确的話，这里对于他給各个經向分布綫都規定了固定

1) 这將是很有趣的，在此指出泊蘭氏（頁 44）直接把 *P. excelsa* Hk. f. 当作 Surrectae 系中种类的“最近的親屬”。这本來將是一个很合邏輯的說法，要不是为了一个事实的存在，那就是在 Pseudapocladus 亞群的進化綫上，并沒有一个舟形的盔的出現，而与此相反，却有着双齒型（Sudeticae）和多齒型（*P. mexicana* Zucc.）的存在。

2) 構造指花部的構造。

的投射綫路这一点，仍然还会有异議的，因为这是很容易以本屬現有分布来加以証明的。这是常識，迁移的大道对于迁移者常常是暢开着的，除了有特殊原因使得軌迹成为單行綫外，就很少理由为什么迁移不会是互通的呢？而这种單行的情形，在植物分布上看来，只在很少的情形下才有的。

来說明这一見解，可以回溯一下几个群的分布軌迹。最先，的确有像他所說的由日本經向綫投射入中国的綫路的。这由西康云南的 *P. tsekouensis* Bonati 和云南四川的 *P. salviaeflora* Franch. 予以証实，这兩种都在分化中心在日本群島的 Gloriosae 系中，找到它們的亲緣連結。在 Sigmantha 群中甚至可以找到更直接的証据。在这里，貴州的 *P. ganpinensis* Vaniot 和日本的 *P. refracta* Maxim. 以台灣的 *P. transmorrissonensis* Hayata 为它們中間的鎖鏈环节。这里所要提醒的是，此处的交通不是單方而是双方的，因为前一例子中，分布趋向是指向西南的，而在后一例子中，趋向是正相反的，因为 Eusigmantha 的原始中心無疑地是在中国本部的西北省份中。

但是这一大道的存在并不意味着它独攬了中国与鄰区間的所有分布交通。事实上，中国和喜馬拉雅所有馬先蒿种类，大部取源自西伯利亜經向綫。無疑地，Sceptrum 群中的大部高級类型都是 *P. tristis* L. 的进化了的后代，而那一种的在西伯利亜的發生，是从沒有引起过問題，而且它的分布也从未伸展到日本去过。在同样情形中的 Neosceptrum 群中的最进化的类型，生于甘肃西康的 *P. recurva* Maxim.，即使不是 *P. proboscidea* Stev. 的直接后代，也是十分亲近的种类，而且同时又都是 *P. striata* Pall. 的間接后代，而这兩种却都是西伯利亜的居戶而后一种在中国北部也很普遍。这几乎是不可想像的，密切地与西伯利亜相接触，中国却必須由日本經向綫来取得所有的馬先蒿的資源。

泊蘭氏也曾肯定喜馬拉雅——云南省区，是西藏——中国省区的投射綫。現在讓我們来看一下到底喜馬拉雅的馬先蒿是从那里得来的呢。在西喜馬拉雅和阿富汗見到的 Comosae 系的一种 *P. brevirostris* Pennell，最与西伯利亜和土耳其斯坦的 *P. dolichorhiza* Schrenk 相近或甚至同种。我們知道 Comosae 系的分布中心是在西伯利亜——土耳其斯坦省区之中。日本只有一种，那是与庫頁島共有的 *P. apodochila* Maxim.，此外还有自东阿尔泰分布至堪察加的 *P. venusta* Schang. 的一个白花变型。在大陆上，这一系所达到的最南的緯度是朝鮮北部，也就是 *P. nigrescens* Nakai 的故乡。再向南連一种都看不到了。这样的处境，就变为多少有些捕風捉影来想像作为 *P. dolichorhiza* Schrenk 的一个新的分化种的 *P. brevirostris* Pennell 之在西喜馬拉雅的存在，是由日本先至西藏——中国而后再由喜馬拉雅——云南繞一个大圈而来的了。迁移的路綫必然是由土耳其斯坦直接南向，經由帕米尔以达阿富汗和西喜馬拉雅的。

同样可以得到啓示的，是来檢查一下 Orthosiphonia 群的分布趋向。它的眞正的原始中心，像以前所推测的，是在西土耳其斯坦，在那里，从 *P. Albertii* Regel 出生了本群的眞正祖先 *P. pycnantha* Boiss. 在一方面，这一种，与 *P. brevirostris* Pennell 采取同一路綫，現在已經达到了西喜馬拉雅的庫那圭，在此現在暂时保持着种的稳定，因为在此从未生出什么較高的种类来。这同一种，另一方面，先进化入于 Abrotanifoliae 系，后来又进入 Myriophyllae 系，在中国北部生下了一个十分活躍的迁移者 *P. alaschanica* Maxim.，这一种在进入中国南部的时候，就变成一个亚种 subsp. tibetica (Maxim.) Tsoong 了。这一亚种更西向推进，現时已达西藏南部。那些大大地进化了的，从这个新的祖先生出来的 Pectinatae 系里的，代表着本群花部發展到頂極的类型，現在在这里，西喜馬拉雅，面对面的遇到了它們的远祖 *P. pycnantha* Boiss. 这种老虎鉗式的 Orthosiphonia 群的分布路綫有力地否定了毫無根据的假定，以为所有喜馬拉雅的馬先蒿的来源，一定要到西康云南区中去找而后者又轉为日本經向綫的投射。

对于日本經向綫就說到这里为止，現在来看一下西伯利亞經向綫投射到高加索省区去的事情是怎样的。無疑地 *P. pycnantha* Boiss. 是有它的西向伸延到伊朗地区去的事实的，但是很显然，虽然是有限度的，Caucasicae 系也有一个东向的对流的，因为这一系的代表种，*P. caucasica* Boiss.，現在也能在伊朗北部找到。然而这比起来还不及我們在土耳其西部找到 *P. olympica* Boiss. 这一点一半那样重要。这一种是 Limnogenae 系中三种中的一种，其他兩种是 *P. limnogena* Kern. 和 *P. recutita* L.[1]。这些种类，是 Flammeae 系和 Hirsutae-verae 系中种类的近亲，它們的生态环境的要求，一定是与那兩个系里的种类極相类似的。我們曉得吐倫——伊朗地区的地貌影响了生态环境，因而是不合于那种含水很高的植物像 *P. Oederi* Vahl 的种类的，所以形成了这个广布种类在这个地区的不存在。以是，这便明白地沒有可能將 *P. olympica* Boiss. 的存在，解釋为因西伯利亞經向綫的投射而由东向西而来。如果反向西面一看，我們找到了在欧洲省区里的 *P. limnogena* Kern. 和 *P. recutita* L.，它們的亲緣关系告訴了我們 *P. olympica* Boiss. 是由什么地方来的。

还有 Eu-apocladus 亚群，那里面無齿的，比較原始的种类，都在欧洲和小亚細亚；仅仅有一种，*P. sajanensis* Steph. 居住在西伯利亚。这一事实，再与后来双齿的 Comosae 系的最大的变化中心，由欧洲移至土耳其斯坦的事实联想起来，使得我們相信馬先蒿的迁移，同样有着一个从欧洲到西伯利亚的东向潮流的。

以上所述，徹底地反証了各个經向分布綫的确定的投射綫路的可靠性；而同时，甚

1) 請参閱后面第二部系統部份中 Limnogenae 系下面的意見。

至以更大的重要性，表明了仅依設法来固定它們的这一事实的本身来講，就成为在生物科学里不正确地来应用統計学的一个例子，这种引用，虽然用意是很好的，但却得到了錯誤的結果。

(五) 地文特征与馬先蒿分布的关系

在討論所有地理分布的項目之前，我們已然提到过忍耐性学說。一个种的忍耐性，当然是它对于各种环境条件的适应性的适应范圍的复合，包括气候的、土壤的以及生物的因素在內，或者换句話說，就是对这些条件的每一种里面的差度的抵抗能力之复合。旣然一个种的忍耐性主要是由它的历史背景塑造而成，所以当我們看到了像本屬中那些群和亞群中所見的在同一遞傳綫中的一些血統很近的亲屬种以及祖先与后代之間，表示着相近似的环境喜好性，就不必表示惊訝了。仅仅在特殊情形起作用时，我們才会看到在一个單位的进化过程里，發生了明显的忍耐性变化，一种不是太不常見，但是在發生时很容易覚察的現象。

在控制植物分布的条件中，气候是被看作第一重要的，而土壤則是紧接着的第二位[1]。这似乎沒有多大必要来着重指出，这些条件是轉受着某一指定的，或大或小的，地区中地文特征的深刻影响的。由于这，地文特征对于植物分布，起着一个間接的，但却是很重大的关系。

在作为馬先蒿的总部的欧亞大陆上，其最特出的自然特征是在于它的南边升起了偉大的喜馬拉雅-阿尔卑斯接連的山脉[2]，成为亞洲內陆的雨障，以及由古泰西斯海的枯竭而成的地中海东部、伊拉克和伊朗的干旱地帶和沙漠[3]。这些大范圍的地文特征無疑地是尖銳地被反映在馬先蒿的分布面积中了。

这几乎是公認的事实，干旱对植物的生命發生一种类似于，但是更深刻于低温的影响。所以从东部地中海至吐倫——伊朗地区的大片的高度干旱地帶的存在，不会不給与欧亞兩洲的馬先蒿分布以一个深刻的影响。分明地，也許由于杂交，已然創造出来了在本屬內其他單位所不見的，具有特殊适应性質的群来[4]。最重要的当然是 Eu-apocladus 了，那个能够抗旱的种的集团，侵入了并且將上面所說的那些干旱的，沒有馬先蒿的地区，占作自己的領域。在較后的年代里，又出現了具有很相类似的生物学特性的 Orthosiphonia。而这兩个單位，一个互叶与一个对叶的，几乎独占了那些对于其他各群

---

1) 参閱戈德，前書頁 361 及以下各頁。

2) 参閱巴孛考克前書，第一部，頁 93—97；也見戈德前書頁 15。

3) 参閱巴孛考克前書，頁 100；戈德，前册頁 18。

4) 参閱吳尔夫(前書 142 頁)提到的卡許卡罗夫和柯罗唯因兩氏的关于植物迁移与环境情况变化之間的关連的見地。

不利的面积。这是可以明显地看出来的，在低緯度的欧洲与亚洲之間的馬先蒿的直接交通，一直是由这兩个單位一同維持着的，而其他單位在这兩洲間的往还，如像 Eurhizophyllum、Eusceptrum 和 Cladomania，都是以繞圈子的路綫，經由环極省区来实現的[1]。一方面它們倆同样地在較暖的云南和喜馬拉雅以及严酷的北極地带中，順利地侵入到其他各群的势力范圍之內去，另一方面又完整地霸占着它們自己的領域，这說明了在植物分布中，干旱是比低温更为有效的障碍。

程度較小，然而也許更为有趣的是在喜馬拉雅的东部和西部的馬先蒿分布現象。这个巨大的山脉的东西兩部，在地文和其他的自然相貌上的区别，是为人所熟知的[2]。現在只剩下了馬先蒿的分布对这些区别的反应如何了。这里可以看出，在兩个賦性很

1) 巴亨考克氏在討論 Crepis 屬的分布时，在 102 頁提到了恩格洛氏对于一个西南趋向的亚欧兩洲間植物迁移路綫的重要性的注意，和他所提出的在冰期中，以及以前和以后的时期中高山植物系的形成的三条通例。三种植物——*Aconitum Anthora*, *Saussurea discolor* 和 *Pedicularis comosa*——被提名来代表許多种类的植物，它們的分布都以它們一方面在阿尔泰，高加索以及阿尔卑斯山的存在，另一方面又見于斯堪的納維亚为其特征。这种的分布的特殊款式是用来証明一种忆說，以为它們在欧洲的存在，是由于一种由阿尔泰至阿尔卑斯山的西南向植物迁移而实現的。

从我們上面所述的論辯中，以及对泊蘭氏的西伯利亚經向分布綫的投射綫路有关的論辯（頁 217）中，这是沒有一絲可疑惑的，那个分布的趋向，至少在 *P. comosa* L.，是正好与恩格洛氏的說法相反的。这是不錯的，*P. comosa* L. 是不見于斯堪的納維亚的，正像他所主張的一样，但是这一事实却并不一定意味着它在高加索与欧洲的存在，是由于一个从阿尔泰向西南方的伸展而使然的。

与原始中心相联系，我們已然提供一个事实（檢閱本文第二續中頁 68, 69 里的論述），那就是在阿尔泰山中，除了我們現在正在談及的群（Eu-apocladus）之外，只有一个互生叶的單位 Eurhizophyllum 了。*P. Oederi* Vahl 和 *P. Albertii* Regel 是后面一群中的兩个代表，而这簡直是不可能来設想这兩种会能在阿尔泰山中生出 Eu-apocladus 来。此外，那無齿型的 Foliosae 系在阿尔卑斯所占的原始中心，以及双齿型的 Comosae 系在东土耳其斯坦的次成中心的不可逆性，更加重了以为 *P. comosa* L. 的迁移趋势是西南向的这一忆說的困难了。

將这一事件放在一般的植物分布和进化的观点下来看，冰川作用，虽然以它們的毁灭性的扰乱，在它們所到之处，消灭了無数的植物种类，但是倒过来，也許以它們在正在迁移中的植物区系后面所不断發生的龐大压力，来促使能于适应它們的祖先所不能适应的环境的新类型——那种除了这样的特殊压力，決不会發生的类型——發生出来。这似乎很清楚地記录在欧亚的馬先蒿的分布款式之中。

像以前已然提及的那样，亚洲所有的些少冰川是不足与欧洲的比拟的。以在西面的大片高度干旱的地域为其障碍，这些在东亚的，因沒有冰川的干豫而悠游的馬先蒿，并沒有生出真能抗旱的类型来，而它們向欧洲扩展它們的分布面积，并不采西南向的捷徑，而是向北先到西伯利亚而后再轉向欧洲。这是最典型地以 Eusigmantha 的 *P. verticillata* L. 为例子的。分明在欧洲的馬先蒿并不如此。受由北方而来的冰帽和阿尔卑斯山的冰川的强烈挤压，于是由旧的北極——高山型的祖先出現一些抵抗干旱的新类型，而这些类型很快地侵入在东边开放着的地域。这个，我相信是为什么会發生这一特殊的群 Eu-apocladus 的理由。所以，單拔馬先蒿来說，事实上是沒有一个完整的自阿尔泰至巴尔干的迁移趋向的；無宁說，一个相反的情形到是确实的。

2) 見潘納尔氏，F. W. 所著的"西喜馬拉雅的玄参科（費城自然科学院，專著第 5 卷，1943）一文中第 2 頁中的論述，以及同頁中下面的附注。在附注中，有一些馬先蒿在东西兩部的比較，但是这些种类之間的亲緣关系，却并未談到。这也是很有趣的，来讀一下 A. C. 喬喜的"喜馬拉雅的植被"，見"印度的前進"杂志第 5 卷（1925），頁 54－58。

不同的——一个喜濕的甚至几乎是水生的 Eurhizophyllum 和一个旱生性的 Orthosiphonia——單位之間的强烈对照来。前者，它的花部構造已然在这一山脉的东段由 Longiflorae 和 Megalanthae 达到了最高峰，在西部明显地显示了一个反頂極的現象。在前一系中，仅只黃花 *P. longiflora* Rudolph (var. tubiformis Tsoong) 由尼泊尔喜馬拉雅西向分布。仅在西部發現的兩种是 *P. Hookeriana* Wall. 和 *P. punctata* Decne.，这是兩个具有显然較在东部的它們的亲屬 *P. siphonantha* Don 的花管为短的类型。在后一系中，存在着类似的情形。住在西部的是 *P. bicornuta* Klotsch、*P. elephantoides* Benth. 和 *P. Hoffmeisteri* Klotsch. 它們在东部的亲緣是 *P. megalochila* L.、*P. megalantha* Don 和 *P. pauciflora* Pennell。無論从花部構造或顏色看来，东边的种类，無可否認地比西边的种类为高超。分明生于西藏东南部的 *P. megalochila* Li 是一个多色的种类，但是 *P. megalantha* Don 和 *P. pauciflora* Pennell 是紅花的。在另一方面，所有西边的种类却都是黃花的。在花部構造上，只有 *P. hoffmeisteri* Klotsch. 可以說是能够与 *P. megalantha* Don 相比拟，而其他兩种則决定地具有不很專化的下唇。在后一群——Orthosiphonia——中，正相反的情形存在着。在东喜馬拉雅，在几个大部是無齿型的种类中只見到很少的进步的类型，那是有長嘴的 *P. oliveriana* Prain 和有中長嘴部的 *P. alaschanica* Maxim. subsp. *tibetica* Tsoong；而这后面的一种，显然是西部所見的进步类型的祖先；在那里，很有一些屬于 Pectinatae 系的具有精巧構造花冠的种类可以見到。

概如上述，这是很易于了解到在适应由很大的地文相貌而形成的大程度的环境特点，并不是由个别的种类，而是由代表整个亲系的集团来实現的。是以对于想找到一个自然系統的分类学家来說，集体地注意到一群种类的忍耐性，是要比注意單独种类的忍耐性为更有深刻的意义了。

(六) 馬先蒿的海拔高度(垂直)分布

已有兩次我們曾經提到忍耐性的学說，和它对于植物地理的重要关系。我們这里要来找出它和海拔高度分布的联系来。要确切地知道这样一种性質复杂的抽象，像某一植物的忍耐性到底是什么的話，即使將那一些与它的生境有关的各項因素都仔細分析，实際上也还是不可能的[1]。但是既然忍耐性是表現于植物本身的适应和喜好某些特殊的生态环境之中，那末，不必做很大的努力，我們可以直接拿生态环境作为一种它的

1) 参观凱因，S. A. 在它的植物地理的基础(1944)，頁 16 內，"环境是通同作用的"題目下的論述。Holocoenotic 这一个字，在生态学名詞里找不到譯义，在这里試譯作"通同作用的"，是否有当，尚待商酌。那段文章的意思，是說环境因为通同作用，所以即使將所有各項因素逐一分析，也無法明了环境对以植物的生理所起的綜合作用的。

忍耐性的籠統的表現了[1]。

这不过是一种常識，高度就是在垂直方向上的，但是压縮了很多的緯度。在这样一种短縮的次序中，人們自然会看到事物也在很短的次序里發生变化了。包含在这一些变化的事物里，当然第一就是气候——一个上面已然提及过的管制着植物分布的首要因素——的很快的变化；而且与此同时，还会有其他相并而来的土壤和生物方面的情况的变化。这就是为什么我們習慣于看到海拔高度控制着分布，永远表現于高山上保持着清晰的植被帶的緣故。所以这里，一个种的受高度限制，至少可以被認为系一个种，在对一个最主要的生态因素方面所表現的忍耐性，也就是对于气候的适应。

至于在一个像馬先蒿这样的分类阶層中某一种类的忍耐性的形成，与它的表現为特殊的高度上的喜好之間的联系，我們可以給予如下的解釋：如果一个种是在很高的緯度上寒冷而潮湿的气候下出生的話，当它南下至低緯度时，我們当然可以想像它將选取很高海拔的地方，在那里它可以找到多少与原来的相接近的气候情況；相反地，如果一个种是在一个天气比較和暖像某些間冰期的稳定时期所有那样情況下出生的話，那末当它向南迁移时，它当然因为受了它的忍耐性的影响的緣故，而習慣地找到气候比較合适于它的低海拔的地方了。至于單种的与种的集群之間的忍耐性关系問題，前面已然談得很詳細，兹不多贅。

在馬先蒿的以前的工作里，对于这一植物分布的特殊項目是很少注意的，但是在这里面我們却希望找到一些从其他分布研究中所得不到的資料。那些文字中所写的，除了告訴我們在某一高度上我們可以找到某一数字的种类之外，沒有其他。为了以它来作为一种媒介，来檢查这一种特殊的分布，与进化、迁移以及系統三方面的相互关系的目的，下面所列一張表，表示以分类次序排列的各群和亞群中的种类的高度分布。每一种后面，有一个包含兩个数目的数字組，这兩个数目分別代表这一种在海拔高度分布的下面的与上面的限度。当一个种只能找到一个記录的时候，那末为了使表格得到它所必需的平衡，就把这个記录的数字，重复一遍，而左右都用同一数字。这里一定要說明，我并不說我这个表格是完备的，事实上与此相差甚远。我并沒有化太大的气力来把所能得到的記录都收集攏来，因为我很知道这并不会損害一点我們希望由这些統計中所能得的效果的。为了比較起来方便起見，还有第二个表格，里面表示了各群及亞群的所有种类的上面的和下面的限度的平均数字。

---

1) 这是可以想像到，一定会有很大的困难的，把很仔細的生态研究来与从比較粗放的地理分布研究得来的結果相并比的。參閱凱因氏前書，頁 7，第二段。

按分类次序排列的表示种的海拔高度上限及下限的表格(以米計)

RHIZOPHYLLUM 群	
EURHIZOPHYLLUM 亞群	
Flammeae 系	
P. flammea L.	50—750
P. Oederi Vahl	300—5100
P. angustiflora Limpr. f.	3960—5335
P. orthocoryne Li	4420—4880
Corydaloides 系	
P. cryptantha Marq. et Shaw	2600—3600
P. corydaloides H.-M.	3200—3800
Pseudo-oederianae 系	
P. pseudoversicolor H.-M.	3600—4700
P. habachanensis Bonati	4100—4200
Rhynchodontae 系	
P. rhynchodonta Bur. et Fr.	3660—4700
Filiculae 系	
P. filicula Franch.	2800—4800
P. Lecomtei Bonati	3500—3500
Macrorhynchae 系	
P. macrorhyncha Li	3660—3660
Robustae 系	
P. Daltonii Prain	4200—5100
P. nepalensis Prain	3900—4200
P. robusta Hk. f.	4800—4800
Macranthae 系	
P. insignis Bonati	4200—4300
P. Klotzschii Hurus.	3600—4500
P. Scullyana Prain	3300—3600
Pumiliones 系	
P. bella Hk. f.	4880—4880
P. Przewalskii Maxim.	4000—4830
Longiflorae 系	
P. longiflora Rudolph	3350—5300
P. chinensis Maxim.	1700—2900
P. armata Maxim.	3000—4600

P. Garnierii Bonati	3000—3600
P. cranolopha Maxim.	2700—4000
P. humilis Bonati	3050—3050
P. Hookeriana Wall.	2700—4500
P. punctata Decaisne	2500—4500
P. variegata Li	4150—4150
P. siphonantha Don	2800—5000
P. tenuituba Li	3080—3080
P. Paxiana Limpr. f.	4300—4300
P. dolichantha Bonati	3200—3200
P. latituba Bonati	3080—3080
P. sigmoidea Franch.	3000—3600
Megalanthae 系	
P. bicornuta Klotz.	2800—5100
P. elephantoides Benth.	2600—3400
P. megalantha Don	2100—4300
RHIZOPHYLLIASTRUM 亜群	
Roseae 系	
P. muscoides Li	3690—5335
Merrillianae 系	
P. Merrilliana Li	3250—4900
P. pulchella Pennell	3000—3150
Asplenifoliae 系	
P. longipedicellata Tsoong	4700—4700
P. Meyana H.-M.	3660—4500
P. Yui Li	4100—4100
P. tsarungensis Li	4000—4000
Paucifoliatae 系	
P. micrantha Li	3100—3100
P. yunnanensis Franch.	3050—4000
P. Forrestiana Bonati	3350—4000
P. microcalyx Hk. f.	3900—4050
Mychophilae 系	
P. mychophila Marq. et Shaw	4000—4900
Franchetianae 系	
P. Franchetiana Maxim.	3660—4900
Pseudomacranthae 系	
P. aschistorhyncha Marq. et Shaw	3400—3600

P. Fletcherii Tsoong	2900-3900
Albiflorae 系	
P. Regeliana Prain	3300—3900
P. rhizomatosa Tsoong	3650—3650
P. perpusilla Tsoong	3600—3600
P. Hicksii Tsoong	4350—4350
P. tapaoensis Tsoong	4700—4700
P. Tayloriana Tsoong	4100—4100
Neolatitubae 系	
P. neolatituba Tsoong	4700—4700
DOLICHOPHYLLUM 群	
EUDOLICHOPHYLLUM 亜群	
Cernuae 系	
P. cernua Bonati	3800—4200
Pseudorostratae 系	
P. chenocephala Diels	3660—4300
P. tatsienensis Franch.	4100—4420
DOLOCHOSTACHYS 亜群	
Pilostachyae 系	
P. pilostachya Maxim.	4720—5070
P. ternata Maxim.	3200—4550
Tantalorhynchae 系	
P. tantalorhyncha Franch.	3050—4000
P. tantalorhynchoides Tsoong	4200—4200
Meteororhynchae 系	
P. meteororhyncha Li	4150—4150
BRACHYPHYLLUM 群	
EUBRACHYPHYLLUM 亜群	
Lyratae 系	
P. stenocorys Franch.	3100—3900
P. cymbalaria Bonati	3400—4400
P. deltoidea Franch.	3200—4200
P. lyrata Prain	4000—4200
P. polyodonta Li	2320—3225
P. lutescens Franch.	3500—4000
Brevifoliae 系	

P. brevifolia Don	3000—3600
P. alopecuros Franch.	2300—4000
P. porrecta Wall.	3900—4500
P. verbenaefolia Franch.	3300—4000
P. Smithiana Bonati	3350—4000
P. Tsaii Li	4000—4250
Debiles 系	
P. Poluninii Tsoong	4400—4400
P. debilis Franch.	2750—2750
P. conferliflora Prain	3850—4850
P. sphaerantha Tsoong	3850—4100
P. tenuicaulis Prain	3950—3950
P. Maxonii Bonati	3000—3000
P. canescens Tsoong	4650—4900
P lamioides H.-M.	3400—4150
P. instar Prain	3600—3900
Integrifoliae 系	
P. integrifolia Hk. f.	2700—4200
BRACHYPHYLLIASTRUM 亚群	
Binariae 系	
P. binaria Maxim.	3900—4000
Urceolatae 系	
P. urceolata Tsoong	3800—3800
P. xylopoda Tsoong	4650—4900
APOCLADUS 群	
EU-APOCLADUS 亚群	
Foliosae 系	
P. Wilhelmsiana Fisch.	1500—2290
P. condensata M. Bieb.	2121—2124
P. atropurpurea Nordm.	2121—2121
Comosae 系	
P. heterodonta Panc	1300—1300
P. comosa Linn.	1242—2727
P. petiolaris Tenore	2100—2100
P. Ferdinandii Bornm.	2050—2300
P. uliginosa Bunge	3800—4000
P. graeca Bunge	1680—1830
P. leucodon Griseb.	1525—2140

P. physocalyx Bunge	
var. *dubia* Bonati	3000—3000
P. achilleaefolia Steph.	4000—4000
P. dolichorrhiza Schrenk	3050—4000
P. gyroflexa Vill.	1500—1500
P. elegans Ten.	2000—2800
P. caespitosa Sieber	1200—2500
P. rostrata Linn.	1200—2300
P. pyrenaica Gay	2000—2200
P. mixta Gren. et Godr.	2000—2200
P. Nordmanniana Bunge	2300—2500
Strobilaceae 系	
P. gracilicaulis Li	3000—3300
P. strobilacea Franch.	3050—3960
P. dichrocephala H.-M.	3350—3450
Oliganthae 系	
P. tahaiensis Bonati	2200—3200
P. cephalantha Franch.	3350—4850
var. *szetchuanica* Bonati	2800—4500
P. longipetiolata Franch.	2800—3600
P. oligantha Franch.	3000—3000
P. tachanensis Bonati	2200—2200
Oxycarpae 系	
P. Monbeigiana Bonati	3000—4200
var. *birmanica* Bonati	3000—3000
P. Stewardii Li	2200—2200
P. tibetica Franch.	4100—4100
P. torta Maxim.	2500—4000
P. Davidii Franch.	2250—3800
Amplitubae 系	
P. amplituba Li	3460—3460
Rhinanthoides 系	
P. rhinanthoides Schrenk	
subsp. *typica* Pennell	3000—4000
var. *labellata* Prain	2750—5500
var. *tibetica* Bonati	3000—5000
PSEUDAPOCLADUS 亞群	
Compactae 系	
P. Orizabae Cham.	3000—4000

P. Parryi Gray	4000—4000
P. mexicana Zucc.	1800—2200
P. similis Heller	2750—2750
P. incarnata Jacq.	1200—2300
Incurvae 系	
P. incurva Benth.	3200—4200
Surrectae 系	
P. attollens A. Gray	1830—3050
ORTHOSIPHONIA 群	
Caucasicae 系	
P. pycnantha Boiss.	2700—5100
P caucasica M. Bieb.	4000—4100
P. cadmea Boiss.	1880—3050
Molles 系	
P. mollis Wall.	3000—4500
Gibberae 系	
P. gibbera Prain	3600—4200
Denudatae 系	
P. polygaloides Hk. f.	3900—4200
P. denudata Hk. f.	3600—3900
Abrotanifoliae 系	
P. obscura Bonati	3660—4270
P densispica Franch.	1880—4270
P. brevilabris Franch.	3500—3500
Platyrhynchae 系	
P. pulchra Pauls.	4000—4000
P. chorgossica Regel ex Maxim.	1525—1830
Myriophyllae 系	
P. subrostrata C. A. Meyer	2100—2300
P. myriophylla Pall. var. *tatarinowii* Maxim.	2100—2300
P. alaschanica Maxim.	1750—3250
P. Chamissonis Stev. var. *japonica* Miq.	1500—3000
P. scolopax Maxim.	3500—4000
P. cristatella Pennell et Li	2580—2750
Pectinatae 系	
P. tenuirostris Benth.	2300—3700
P. pectinata Wall.	2100—4400

P. Stewartii Pennell	2400—3700
P. rhynchotricha Tsoong	3700—3900
P. cyrtorhyncha Pennell	2000—4300
P. pyramidata Royle	2700—5000
subsp. *kashmirica* Tsoong	2000—4500
subsp. *multiflora* Tsoong	1700—2600
Gyrorhynchae 系	
P. gyrorhyncha Franch.	2750—3350
P. Wangii Li	2700—3600
P. Duclouxii Bonati	3400—4300
Semitortae 系	
P. Oliveriana Prain	3600—4300
P. semitorta Maxim.	2500—3500
SIGMANTHA 群	
NOTHOSIGMANTHA 亞群	
Cheilanthifoliae 系	
P. cheilanthifolia Schrenk	3300—4900
P. ophiocephala Maxim.	3400—5100
P. globifera Hk. f.	3350—4500
Curvitubae 系	
P. anas Maxim.	3000—3900
EUSIGMANTHA 亞群	
Plicatae 系	
P. plicata Maxim.	2900—3500
P. luteola Li	3660—3660
Verticillatae 系	
P. rupicola Franch.	2745—4800
P. Roylei Maxim.	3300—5000
P. Shawii Tsoong	4500—4500
P. nana C. E. C. Fisch.	4000—4920
P. anthemifolia Fisch.	2000—2500
P. violascens Schrenk	4000—4300
P. nodosa Pennell	5000—5000
P. Chingii Bonati	3000—4200
P. kansuensis Maxim.	1825—3850
P. szetschuanica Maxim.	4450—4550
P. involucrata Tsoong	3300—3600
P. dolichostachya Li	3660—3660

P. diffusa Prain	3300—3900
P. stenotheca Tsoong	3950—3950
P. verticillata Linn.	2100—3350
P. tangutica Bonati	1380—2500
P. refracta Maxim.	1300—1300
P. brachycrania Li	3700—3700
P. likiangensis Franch.	3200—4600
P. lineata Franch.	2800—4570
P. holocalyx H.-M.	2000—2000
P. spicata Pall.	1500—2500
P. Taquetii Tsoong	1700—1800
Microchilae 系	
P. microchila Franch.	2750—4000
RIGIOCAULUS 亚群	
Salicifoliae 系	
P. salicifolia Bonati	900—3500
Rigidae 系	
P. comptoniaefolia Franch.	2400—3000
P. rigida Franch.	2500—3000
P. Mairei Bonati	2500—2600
CLADOMANIA 群	
Hirsutae-centripetae 系	
P. Langsdorffii Fisch.	170—500
Canadenses 系	
P. canadensis Linn.	1600—3200
P. crenulata Benth.	2300—2450
Palustres 系	
P. sylvatica Linn.	90—300
P. lusitanica Conth.	600—1200
P. numudica Pomel	20—120
P. palustris Linn.	370—370
P. labradorica Wirsing	130—900
Racemosae 系	
P. lapponica Linn.	7—1200
P. resupinata Linn.	300—1600
P. racemosa Dauglas	30—2200
Carnosae 系	
P. nigra Bonati	1100—2100

P. Collettii Prain	1200—1500
P. corymbosa Prain	1200—1200
P. veronicifolia Franch.	1600—2600
P. kouytchenensis Bonati	2800—3350
P. Tsiangii Li	466—466
P. crenata Maxim.	3350—3350
P. zeylonica Benth.	1800—2100
P. bifida Pennell	900—2100
Microphyllae 系	
P. tenuisecta Franch.	1500—3660
P. Henryi Maxim.	400—1420
P. Labordei Vaniot	130—2500
Polyphyllatae 系	
P. Stadlmanniana Bonati	2440—3050
P. kariensis Bonati	3960—3960
P. pinetorum H.-M.	2500—2800
P. Limprechtiana H.-M.	2100—3400
P. gruina Franch.	2600—3000
P. polyphylloides Bonati	3300—3400
Furfuraceae 系	
P. Hemsleyana Prain	2900—4000
P. furfuracea Wall.	2400—3600
P. Pantlingii Prain	3500—4200
P. taliensis Bonati	2750—3350
CYATHOPHORA 群	
Reges 系	
P. rex C. B. Clarke	2500—4300
P. Lipskyana Bonati	1930—3800
P. thamnophila Li	3200—3500
P. cupuliformis Li	4000—4000
Cyathophylloides 系	
P. cyathophylloides Limpr. f.	3850—3850
Superbae 系	
P. superba Maxim.	2800—3900
Cyathophyllae 系	
P. connata Li	4150—4150
P. cyathophylla Franch.	4700—4700

DOLICHOMISCUS 群	
PTERIDIOIDES 亚群	
Pteridifoliae 系	
P. pteridifolia Bonati	800—1600
Phaceliaefoliae 系	
P. phaceliaefolia Franch.	1600—1850
P. Fargesii Franch.	1400—3800
EUDOLICHOMISCUS 亚群	
Acaules 系	
P. Artselaeri Maxim.	1100—1500
Vagantes 系	
P. vagans Hemsl.	950—2200
Longipedes 系	
P. nasturtiifolia Franch.	2000—2000
P. longipes Maxim.	4100—4100
P. axillaris Franch.	2750—3350
P. filicifolia Hemsl.	2500—3200
Omiianae 系	
P. omiiana Bonati	2300—3200
Muscicolae 系	
P. macrosiphon Franch.	1200—3500
P. geosiphon Smith et Tsoong	3500—3900
P. muscicola Maxim.	1750—2650
CYCLOCLADUS 群	
EUCYCLOCLADUS 亚群	
Salviaeflorae 系	
P. salviaeflora Franch.	2000—3900
Melampyriflorae 系	
P. floribunda Franch.	2700—2700
P. melampyriflora Franch.	2700—3600
P. pseudomelampyriflora Bonati	3050—3050
Longicaules 系	
P. longicaulis Franch.	3660—3880
P. Dielsiana Bonati	2135—2135
Graciles 系	
P. gracilis Wall.	1800—3900
P. khasiana Pennell	1200—1900

NEOSCEPTRUM 群

EUNEOSCEPTRUM 亜群

Striatae 系

P. striata Pall.	1300—2990
P. Grayi A. Nelson	2600—2800
P. mandshurica Maxim.	1205—1205

Recurvae 系

P. recurva Maxim.	3250—3600

SCEPTRUM 群

EUSCEPTRUM 亜群

Gloriosae 系

P. Sceptrum-carolinum	400—500

Grandiflorae 系

P. grandiflora Fisch.	350—400

Tsekouenses 系

P. tsekouensis Bonati	3050—4200

Tristes 系

P. shansiensis Tsoong	1400—1800
P. tristis Linn.	2750—3050

Caleatae 系

P. galeata Bonati	4000—4270

Rudes 系

P. Fischeriana Tsoong	3333—3333
P. rudis Maxim.	2350—3350
P. princeps Franch.	2800—3370
P. Dunneana Bonati	2440—4000

Imbricatae 系

P. Clarkei Hk. f.	3600—4500
P. platychila Tsoong	4600—4600
P. mucronulata Tsoong	2600—2600
P. imbricata Tsoong	4600—4600

Dolichocymbae 系

P. dolichocymba H.-M.	3500—4300

Ingentes 系

P. pseudosteiningeri Bonati	3000—4300
P. trichocymba Li	2745—4730
P. ingens Maxim.	3050—3900

Trichoglossae 系	
P. trichoglossa Hk. f.	3600—5000
P. rhodotricha Maxim.	3660—4000
Lasiophrydes 系	
P. craspedotricha Maxim.	3400—4500
P. lasiophrys Maxim.	3400—4750
P. cinerescens Franch.	4000—4400
Kongboenses 系	
P. kongboensis Tsoong	4000—4000
P. retingensis Tsoong	4200—4200
Excelsae 系	
P. Vialii Franch.	2700—3600
P. excelsa Hk. f.	3600—3600
Kialenses 系	
P. kialensis Franch.	3050—4875

表示各个群及亞群的海拔高度的上限和下限平均数的表格(以米計)

RHIZOPHYLLUM 群	
EURHIZOPHYLLUM 亞群	3206—4128
RHIZOPHYLLIASTRUM 亞群	3735—4188
DOLICHOPHYLLUM 群	
EUDOLICHOPHYLLUM 亞群	3853—4306
DOLICHOSTACHYS 亞群	3864—4394
BRACHYPHYLLUM 群	
EUBRACHYPHYLLUM 亞群	3433—4022
BRACHYPHYLLIASTRUM 亞群	4116—4233
APOCLADUS 群	
EU-APOCLADUS 亞群	2479—3109
PSEUDAPOCLADUS 亞群	2540—3214
ORTHOSIPHONIA 群	2730—3731
SIGMANTHA 群	
NOTHOSIGMANTHA 亞群	3263—4600
EUSIGMANTHA 亞群	3001—3700
RIGIOCAULUS 亞群	2075—3025
CLADOMANIA 群	1531—2277
CYATHOPHORA 群	3766—4025

DOLICHOMISCUS 群	
PTERIDIOIDES 亞群	1267—2417
EUDOLICHOMISCUS 亞群	2215—2960
CYCLOCLADUS 群	
EUCYCLOCLADUS 亞群	2406—3133
NEOSCEPTRUM 群	
EUNEOSCEPTRUM 亞群	2088—2648
SCEPTRUM 群	
EUSCEPTRUM 亞群	3077—3740

現在讓我們来檢視一下上面所列的表。第一步自然应該先来比較一下那兩个代表群 Rhizophyllum 与 Sceptrum 所占的高度是怎样的。

在第二个表中，我們看到在 Eurhizophyllum 和 Eusceptrum 后面的数字組，各自地記录了 3,206—4,128 米和 3,077—3,740 米的高度。表面上看来，这些数字显示了 Rhizophyllum, 作为一个眞正的北極——高山性的單位，所占的高度在与 Sceptrum 比較下却幷不高出多少。但是我們不要为这些数字所欺騙，因为在細究之下，我們会發覺它們在某一程度上是使人誤解的。某些因素促使这兩群的高度分布的眞面貌起了一些变化。

要找出这些因素来，第一个表示种类的高度的表是須要檢看的。在 Eurhizophyllum 下面，有兩种是在極低的高度上生長的，那就是 *P. flammea* L. 和 *P. Oederi* Vahl, 它們的数字組分别表示着 50—750 米和 300—5,100 米的高度。这些数字的特出点是在于在前一种中的兩極端之間，仅仅相差 700 米，而在后一种中則差数突然高升到 4,800 米之多。在这里相差是特出的，但是其实这幷不是什么不可理解的現象，如果我們拿这些数字来与这兩种的分布面积相比較一下。我們知道前一种是限生在北極和亞北極地帶的而后一种現在已經把它的分布面积远推至欧洲的阿尔卑斯山和亞洲的喜馬拉亞山了。这种事实只能意味着 *P. Oederi* Vahl, 作为 Rhizophyllum 群中所有的高等类型的眞正的祖先，在这一群剛一开始的时候，就以它在离开了环極省区的原始中心之后，經常选取愈来愈高的海拔这一点来表示这一群的对于北極——高山气候的肯定的喜好。在这里，北極种类的很低的海拔高度数字，如果放在别的低海拔的群中时，会不知不覺地混入其他的数字中去，然而到了像 Rhizophyllum 一样的高山群中，就会变成一种特点而同时也將減低了这一群的海拔平均数字。

在同一亞群中，絕大部份的种类是像 *P. Oederi* Vahl 一样地愛好最高的海拔，而其中共有五种是在 5,000 米以上發見过的，这个数目是本屬中其他各群所不能超过的。这一事实告訴了我們，作为一个單位，Eurhizophyllum 是特别适应高山寒冷生活的。

但是，在我們的表里总共有7个种下降至3,000米以下的海拔上来，它們是 *P. filicula* Franch.、*P. chinensis* Maxim.、*P. siphonantha* Don、*P. cranolopha* Maxim.、*P. bicornuta* Klotsch.、*P. elephantoides* Benth. 和 *P. megalantha* Don。这7种里面，*P. filicula* Franch. 沒有下到比 3,000 米低多少的地方来，而它的上面的界限，还是靠近 5,000 米。其余的6种則侵入到更低的海拔上来，在这中間 *P. chinensis* Maxim. 和 *P. megalantha* Don 下降最低，它們各自地在中国北部的1,700米的山上和喜馬拉雅南坡2,100米处被看到。这一現象指示給我們在 Eurhizophyllum 中的前进类型中有着一个走向低海拔的趋势。显然这一趋势，在距 Flammeae 系还不很远的进化阶段上的 Filiculae 系中已然开始，然而还不很明显，但是到了这一群現在进化高峰的代表系 Longiflorae 和 Megalanthae 的时候，就变成十分特出了。这里又是另一个使 Eurhizophyllum 的海拔高度数字的平均减低价值的因素[1]。

現在將我們的注意轉移到 Eusceptrum 去。在發軔的 Gloriosae 系中的种类和与它紧密相連的 Grandiflorae 系都是低海拔的植物，生在500米以下的地方。在 Tristes 系中，我們所記的兩种已經稍稍升高，它們的下限1,400米，为 *P. shansiensis* Tsoong 所占，和3,050米的上限，为 *P. tristis* L. 所占。从这里以上，各系的所有种类所占的垂直位置虽然不大稳定，却繼續地升高了，一直到这一亞群到了 Lasiophrydes 和 Kongboenses 兩系，那里一个特高的6,000米的限綫为 *P. lasiophrys* Maxim. 所达到，而其平均数字，也都比4,000米为高。由此观之，Eusceptrum 里面也有着一种更变海拔高度喜嗜的趋势，是十分明显的了，虽然这里的变化，分明是与 Rhizophyllum 取相反的方向的。在 Eusceptrum 里这一趋势的早期發現，使这一亞群的垂直分布的数字，大大提高；这再与和它对立的亞群里的相反的趋势，使得这兩个單位的数字，几乎兩兩相等。显然地，在它們各自的开端处，至少在它們的海拔高度的喜好方面，它們是相差得極显著的，但是当它們的成員进入新的地区的时候，因为新鮮环境的接触，先开始了而且后来又促进了它們的进化步伐，而与此同来的是原来的忍耐性的改变，这充份地反映在所形成的新类型对于海拔高度的适应性上。更有趣的是我們还再一次地找到 Eusceptrum 中的最复杂的类型 *P. Vialii* Franch. 和 *P. excelsa* Hk.f.，占有比 Trichoglossae、Lasiophrydes 和 Kongboenses 系低得很多的海拔高度，必然为一种在达到上升的極限后再次改变忍耐性的明显标志。

---

1) 以另一方法来証明这一事实，我們可以看一下完全在低緯度中發生和进化的，并且也沒有降低海拔高度的迹像的 Rhizophyllum 的另一支派 Rhizophylliastrum 亞群的数字。这里的数字值，是要比 Eurhizophyllum 高得很多了。

現在再来看一下那些次成的群和亜群。在第二表中，我們看到主要受 Flammea-型影响的 Dolichophyllum 对叶群，有着甚至高于 Eurhizophyllum 的数字組，就是 3,853—4,306米。这些数字無疑地是会很近乎那个原始單位的数字的，如果把后者里面的低海拔的种类除去的話。与前面相反的，在那些主要由 Capitata-型来影响的群和亜群，如 Dolichomiscus、Cyclocladus 和 Neosceptrum 等等的海拔高度数值却低得很多，它們的下限是在 Pteridioides 亜群下的1,267米，而上限，是 Euneosceptrum 亜群所表示的2,648米。

在那些不易判断而間接出生的群，我們看到在 Eu-apocladus、Orthosiphonia 和 Cladomania 下面的平均数目組是：2,479—3,109米、2,730—3,731米和1,531—2,277米。在这里显然是多余的来指出前面兩个数字較高的是靠近 Rhizophyllum 的，而最后具有最低数字的群，是与 Sceptrum 比較亲近。甚至于在一个單位里面像 Sigmantha 群所表示的，也与上面的这些例子如出一轍。这里，可能由 Orthosiphonia 得来的 Nothosigmantha 的数字組是 3,263—4,600 米，从 Cladomania 而来的 Rigiocaulus 是 2,075—3,025 米而那个最模棱兩可的 Eusigmantha 是 3,001—3,700 米，这是正好可以楔入前面兩組之間的一个数字組。更有足以詫异的是在 Eusigmantha 里面的唯一代表系 Verticillatae 內，那三个"种的集群"也保持着約略相同的比例。在此处，那些与 Nothosigmantha 相近的种类如 *P. rupicola* Franch.、*P. Roylei* Maxim.、*P. nana* C. E. C. Fisch. 和 *P. likiangensis* Franch. 保持着最高的数字；那些与 Rigiocaulus 亲近的如 *P. verticillata* L.、*P. tangutica* Bonati、*P. refracta* Maxim. 和 *P. spicata* Pall. 則表示出最低的数目来，而那些中間类型如 *P. szetschuanica* Maxim.、*P. diffusa* Prain、*P. involucrata* Tsoong 和 *P. lineata* Franch.，則显示中間的数字。

根据由比較形态推論而来的亲緣关系，我們的新系統將要有一个最特出的，也可能是唯一的面貌，在它的輳合的性質上，而这是完全与本屬的进化特点符合的，而我們的系統安排也將把尖銳的劈綫放在兩端，以 Rhizophyllum 和 Sceptrum 为代表，而將所有其他的派生群放在中間。从上面的統計看来，我們的讀者是不会看不見在本屬的各个群与亜群中的海拔高度分布的性質，与我們系統的特出点保持着多么緊密而徹底的相互关系。而且这种相互关系不單是存在于以屬为單位之下的大分类單位（群）的水平上，而且同样地在更低的水平上存在，如像一群中的亜群或甚至于在像 Verticillatae 系中的三个"种的集群"中。这种在忍耐性与亲緣关系之間隐藏着的关連，为海拔高度所揭示出来的事实，是实在可以惊异的。

垂直分布的数值是在这里正面地用来証实我們系統的自然亲緣的性質，但是也正可以同样地用来找出系統中的缺点来。举例說，*P. salicifolia* Bonati 因表面上与 *P.*

integrifolia Hk. f. 的相似曾被李惠林氏联合成为 Holophyllum 組。在我們的表中，前者的海拔高度值（可在 Sigmantha 群中的 Rigiocaulus 亞群中找到）是 900—3,500 米[1]而后者（可在 Brachyphyllum 群中的 Eubrachyphyllum 亞群中找到）是 2,700—4,200 米。除了由形态的观点得来的理由之外[2]，我們仅以拔海高度的不同，就有足够的理由来把这兩种認为系亲緣上很远的种类。这是很容易見到的，由于这兩者被武断地放在一起时所發生的它們在拔海高度的数字上的不調和性，当它們被分拆开来而各自地被放入 Rigiocaulus 和 Eubrachyphyllum 之后，就立即消失了。同样的情形，也在李氏系統中所給与 Muscicolae 和 Longiflorae 兩系的地位中存在着。

除了上面所述的以外，还有别的有趣之点在我們的馬先蒿拔海高度分布的研究中被揭示出来。第一，这是确定地可以証明的，凡相近的种类，常常生在相似的高度上，但对于高度的偏好有所改变，是常时發生的事情；同时，这种改变大多在漸漸而来的情形下發生，而且，如果一旦發生后一般都采取一定的方向而沒有很大的搖惑不定的情形，不是向高处就是向低处，一直等到到了一个也許是由这个單位的集体忍耐性所控制的限度之后，那时可能又有一个相反方向的改变。因为这样的緩慢的变化，占着一个單位的进化行列中相去較远地位的种类，就可能居住在相差很远的高度上。第二，一般說来，一些种如果有着較寬范圍的海拔分布，也就常常同时是在地理上有着較寬面积的种类，例如 *P. Oederi* Vahl、*P. longiflora* Rudolph，等等。在 Eucyclocladus 里面，只有 *P. gracilis* Wall. (1,800—3,900 米) 自云南分布至阿富汗。这种相互关系显然是因为这些种类有着較大忍耐性范圍的緣故。

最后，这是值得在这里提及的，海拔高度所能給与我們的任何服务，只有在它們与系統相配合而在亲緣观点之下同时研究才能实現[3]。將相近高度上的种类随意归在一起是沒有多大意义的，这是最明显地为 Rhizophyllum 与 Sceptrum 兩群所标榜出来。因为前者的下降和后者的上升，这兩个相对的群中的种类，迟早是必不可免地要在某些海拔高度上相遇的。所以这是很难于对一个把种类仅因生在同一高度上而排列在一起的表格，作出任何評价来。（待續）

1） 这个数字組內的上限度，似乎高了一些。正像表中其他种类中的高度記录一样，可能是不准确的，不过我們除了用它外，沒有别的办法。

2） 参看后繼的第二部分类系統中 Rigiocaulus 亞群下的說明。

3） 我在这一題材中的做法，与万斯坦尼斯（“馬来山地植物区系的来源”，这一本書現在找不到来作参考）所表示的意見，曾被凱因氏（前書 269 頁）与“成对的类型及其分布面积”相联系而提到过。我們的研究，很确定地表示了在种类的高度之間的比較，是可以很有益的，虽然它的結果如何，全要看兩相比較的种类的关系是否准确而定。但把沒有極近亲緣的种类来相比是不会得到什么有价值的結果的，但这也并不就意味着所有这类比較都是無意义的。

A NEW SYSTEM FOR THE GENUS *PEDICULARIS* (CONTINUED)

TSOONG PU-CHIU

(*Institute of Botany, Academia Sinica*)

The center of origin of *Pedicularis* (continued)

We have arrived by the foregoing reasoning, in complete accord with Prain, at the conclusion that the center of origin for *Pedicularis* is in the Circumpolar Province. Yet, bounded within the circle marked by the summer isothermal of 15°C is a vast area, one that is far too vast for any feeling of exactitude. We must, therefore, try to see if there is any possibility of narrowing down this vast area to a smaller one which, by its compactness, may then offer us an idea in better precision.

With such a purpose before us, a more attentive re-examination of the distribution of all archaic forms[1] becomes imperative, for such forms, being the forerunners of leading groups, are alone in a position to bear something on the subject. To meet such a requirement, only five species found in Polar regions are to be brought into consideration, namely, *P. flammea* L., as the initiator of *Rhizophyllum*, *P. capitata* Adams, as that of *Sceptrum*, *P. hirsuta* L. and *P. lanata* Cham. et Schl. as those of *Apocladus* and finally *P. Langsdorffii* Fisch. as that of *Cladomania*. In trying to locate more accurately the areas of these species, I find Hulten,[2] with his admirable work, to be my reliable authority on a number of species. For convenience sake, it is perhaps better to disregard the order of importance and to quote first from him the geographic areas of three species as following:

---

1) Just to reassure ourselves of the soundness of the basis upon which are founded our arguments, it is pertinent to refer back once more to our discussions in Morphology and Phylogeny. We have arrived there at the irrefutable results about the progressive floral sizes in *Rhizophyllum* and the consecutive developmental stages in the length and position of the lower lips in *Sceptrum*. Thus, with the rather small flowers of *P. flammea* L. as a basis, it seems improbable, in view of the physical limit of floral construction, that there ever existed in *Rhizophyllum* forms which were any more primitive than this spceies. Similarly, by the rather apposed position and the very shortness of the lower lip in *P. capitata* Adams, it is perhaps safe to infer that *Sceptrum* never possessed in its history any form with more archaic type of corolla. Furthermore, by the progressive stages in the sequence of *P. flammea* L., *P. Oederi* Vahl, *P. pseudo-versicolor* H.-M., *P. habachanensis* Bonati, *P. rhynchodonta* Franch., *P. filicula* Franch., *P. robusta* Hk. f., *P. bella* Hk. f., *P. longiflora* Rudolph and *P. megalantha* Don, we can almost be sure that the phylogenetic line in *Rhizophyllum* bears scarcely any mark of interruption; so is the chain of descent in *Sceptrum* remaining intact as is in the order of *P. capitata* Adams, *P. Sceptrum-carolinum* L., *P. tristis* L., *P. galeata* Bonati, *P. dolichocymba* H.-M., *P. trichoglossa* Hk. f., *P. Vialii* Franch. etc.

2) Hulten, E.: Flora of Alaska and Yukon, IX (1949), *Pedicularis*, pp. 1401-1420.

1. *P. capitata* Adams: Asia: from the mouth of Yenisei R. eastward over Taimyr land and along the coast to Chukch Penins., south to Penshina, S. Kamtchatka and Paramushir I. America: from Alaska and Yukon over Victoria Land, Melville I. and N. Ellesmereland to S. Baffin Land, south to mts. of S. E. British Columbia (p. 1403).
2. *P. lanata* Cham. et Schl.: Europe: Spitzbergen, Nova Zembla, Vaigatch, the northern Urals. Asia: from the Urals to Chukch Penins., south at Yenisei to about 59° N., to Yakutsk distr. and the northern Kurils (Paramushir I.), isolated in Dschungarski Alatau (acc. to Krylof). America: from Alaska and Yukon over Banks Land, south to Queen Charlotte Is., southern British Columbia, northern Hudson Bay and N. W. Labrador Penins., N. W. Greenland (p. 1408).
3. *P. Langsdorffii* Fisch.: from Taimyr to Wrangell I., Herald I. and Chukch Penins., south to Karaginsk I. America: Alaska and Yukon over Banks Land and Ellesmereland to N. W. Baffin Land, south to the Arctic mainland Coast, N. W. Greenland (p. 1409).

Now let us see the ranges of the two other species, *P. flammea* L. and *P. hirsuta* L. The area of the former, according to Limpricht, is found to embrace part of northern Canada (northern Rockies and to the north), Labrador, Greenland, Iceland and Lapland; that of the latter, Labrador, Baffin Land, Ellesmereland, northwestern and eastern Greenland, Spitzbergen, Lapland, Novaja Zemlya, and regions along the rivers Yenisei, Taimyr, Olenek and Lena.

In the above, apart from *P. lanata* Cham. et Schl., whose fairly complete holarctic distribution gives us little information about its migratory direction, all the other species, with their migratory tracks variously disrupted, seem to offer us something worthwhile from certain similarities and dissimilarities in their distribution. *P. capitata* Adams and *P. Langsdorffii* Fisch. are found to range the breadth of arctic America westward continuously to Yenisei and Taimyr regions respectively in arctic Siberia, but are absent in arctic western Siberia and arctic Europe. It may be noted here that they both have Greenland as their easternmost point of distribution. As to the two other species, *P. flammea* L. and *P. hirsuta* L., their areas show only minor differences between themselves, but are quite dissimilar to those of the two preceding species. In the New World, they both occupy, though somewhat differing in extensiveness, part of eastern arctic America; in the Old World, the former has its range mainly limited to Lapland while the latter has extended eastward to the Lena River region. They are absent from eastern arctic Siberia and

western arctic America (at least not found in Alaska and Yukon). The point of interest here is that irrespective of the differences in their areas, these five species are found to be represented in the flora of Greenland. Now we would like to take this opportunity to remind our readers about the hypothesis of a diphyletic origin of the genus presented in the first part of this paper, a hypothesis which demands the emergence and simultaneous existence at a location of the primordial types of the two representative groups, *Rhizophyllum* and *Sceptrum*, with their subsequent inter-crossing resulting in the issuances of certain secondary, yet still primitive forms which initiated the derivative groups. Now Greenland seems to be the very location which answers adequately such a requirement, as it must be difficult to regard the concentration of all these primitive forms on the island to be sheerly fortuitous. I think that few would object to my view in regarding these five species as the respective forebears of the four leading groups, although some of them would perhaps be less willingly persuaded into the belief that the latter three species are of hybrid origin. It seems now evident that a closer examination of the areas of these primitive species has actually responded us with an answer that the *exact* center of origin for the genus is in Greenland. I strongly suspect that this is a right answer to our question. For a clearer conception of my idea, it is well to reshuffle the arrangement of localities in the areas of these species into a more appreciable order as following:

1. *P. flammea* L.: from Greenland westward to Labrador and the Canadian Rockies; eastward, it went through Iceland to Lapland.
2. *P. capitata* Adams: from Greenland westward to Ellesmereland, southward to Baffin Land; from Ellesmereland southwestward through Malville Island, Victoria Land to Great Bear Lake, thence one track leading south to south-east British Columbia, the other leading west to Yukon and Alaska, crossing the strait to Chukchi Peninsula wherefrom the line of dispersal leading directly to Yenisei River region.
3. *P. hirsuta* L.: from Greenland westward to Ellesmereland, southward to Baffin Land and Labrador; from Greenland eastward to Spitzbergen and Lapland, the former line leading through Novaya Zemlya to the Siberian Mainland and the latter line simply extending eastward and the two coming to meet at Yenisei; thence through Taimyr and Olenek regions to end ultimately at Lena River region.
4. *P. lanata* Cham. et Schl.: from Greenland southward to Labrador and northern Hudson Bay, northwestward to Banks Land, westward to Yukon,

veering south, the tracks coming to Queen Charlotte Island and southern British Columbia; from Yukon westward, it comes to Alaska; from Greenland eastward, it passes through Spitzbergen, Novaya Zemlya and Vaigatch to arrive at the northern Urals; further east, the track extending through Yenisei River region to Yakutsk, and stopping presently at the Kurils[1].

5. *P. Langsdorffii* Fisch.: from Greenland to Ellesmereland, southward to Baffin Land, southwestward to Banks Land, again southward to Yukon, turning west, it passes through Alaska; after crossing over to Chukchi Peninsula, one line going southwest to Karaginsk Island and another northwestward to Wrangell and Herald Islands with the main line running strictly to Taimyr Land.

From the above, it is more than apparent that if Greenland is taken as the exact center of the genus, a perfect pattern of distribution of the species in closest coordination with the phyletic developments will be the result. Of course, closely following such an assertion, there will be the problem of how these species came to be on Greenland, since their range is manifestly incompatible with the physiographic position occupied by the island to-day. For this, we will have something more to say; but it will be under quite a different subject.

C. The chronology of *Pedicularis*

In inquiring into the chronology of *Pedicularis*, there are two important points to clarify, namely, the antiquity of the genus itself as a unit and the chronological orders of the various major subdivisions it embraces.

Regarding the antiquity of the genus, Limpricht (p. 161) has suggested that it came into being at the end of Cretaceous stage or at the beginning of Eocene. Prain, though without making any definite commitment, seems to hint a much later age, since his discussions in geographical distribution concern mainly with the Ice Age. To prove such presumptive antiquity, the most direct and reliable evidences must come from palaeobotanical data, yet in this respect, *Pedicularis* is sadly destitute of fossil records[2]. Upon such unfortunate condition, the only way to get any idea about the age of the genus is to resort to indirect inferences which may

1) The track of dispersal of *P. lanata* Cham. et Schl. in eastern Siberia apparently leads southeasterly to Kurils rather than strictly eastward to Anadyr, so the two tracks——one eastward and one westward from the common center in Greenland——do not come to joint themselves at Bering Strait. Such an arrangement seems to favour the view that its center of origin is in Greenland.

2) Cf. Limpricht's reference (l. c. 161) to the only record about *P. sylvatica* L. mentioned by Pax, in his "Pflanzengeographie von Polen" (Berlin, 1918), p. 28.

be derived by comparing certain peculiarities in present distribution to the secular changes in continental outlines that are known to have happened in past geological epochs. Now we are already in possession of the knowledge that the exact center of origin is in Greenland, we may take advantage, with the peculiar physiographic position occupied by the island to-day, in making a good use out of it. We are going to ask once more the question about how these species came to exist on the island.

In the face of such a question, it is imperative to settle first whether it is possible that the *Pedicularis* species, as well as other plants in the floras of Greenland, and other islands as Iceland and Spitzbergen, are adventive in character, being the result of immigration from the mainlands. This, in turn, immediately introduces another interesting problem regarding the effect of glaciation on the vegetation of these islands. Matthew, in his "Hypothetical Outlines of the Continents in Tertiary Times"[1], discusses the matter under Pleistocene Epoch. There he asserts that possibly the glaciers in Greenland had been so extensive as to reach beyond the borders of the land on all sides, thus might have by its sweeping effect wiped out whatever life inhabiting the island before the glaciation. If the assertion is true to fact, then we must regard these *Pedicularis* species as post-glacial immigrants rather than the components of an autochthenous flora of the island. Let us see the facts. I doubt that anybody would believe in the possibility of seeds coming from the east by crossing the wide expance of seas between the European Continent and Greenland. Of course, we must reckon with the chance dispersal of seeds; but it is only possible in the cases of a single or only a very few species within any given genus, but not as many as seven species of *Pedicularis* to be counted now in the present vegetation of Greenland which is supposed to have replaced the one that had been denuded altogether by the acts of ices. The only chance for the dispersal of so many species within a single genus is therefore from the west, i.e., from the continent of North America. But plainly, distributional peculiarities do not allow such a simple interpretation, as it calls for conjecture which is to a great degree incredible. Take for instance the areas of two species, *P. flammea.* L. and *P. hirsuta* L. If they are supposed to have been originated in Europe, then, being stopped by the sea in the west, their presence in eastern arctic America including Greenland must be attributed to an eastward extension from Europe. But how are we to give an explanation to their complete absence in eastern arctic Siberia and western

1) This artical was published in Bull. Amer. Mus. Nat. Hist. XXII, pp. 353—383 (1906). The maps were reproduced by Babcock, l.c.

arctic America? No worldly causation is known to exert such tremendous effect on plant species as to wipe out their whole populations on such extensive areas without leaving here and there any relics, not even the acts of glaciations. Even glaciation can perform miracle like this, still our palaeogeographical knowledges defy such a conjecture, as Asia is among the continents that suffered least from the actions of ice in the Quarternary Times. If it is assumed that they made their appearances first in the North American Continent, then there is still the same difficulty to interprete their present ranges in Lapland and Scandinavia.

Now there is a diametrically opposed view held by Limpricht who expresses it thus in page 162: "Für Island ist während der Ancylus-Zeit ein warmes Klima nachgewiesen, bei dem das nördliche Ufer wärmer als jetzt das westliche, und auch auf Spitzbergen hat in der Postglazielzeit ein milderes Klima geherrscht als heute. Spitzbergen war wahrscheinlich eisfrei und daher ist es erklärlich, dass die genannten Arten in Grönland und Spitzbergen die Eiszeit überdauerten." It seems to me to be an infinitely more plausible answer to the present distribution of *Pedicularis* on these islands[1], because it settles the problem that the island dwellers of nowadays are the heirs of the selfsame species that were found there prior to the glaciations, although it has by no means satisfied the question as to how these species came to be on Greenland, since the sea has served as an unsurmontable barrier to their passage in the east, while in the west, great tracts of land here and there devoid of any traces of these species in their respective ranges make the explanation of their having come from the west seemingly ridiculous. How are we to get our answer if their presence in Greenland can be attributed neither to a westward migration from Europe nor to an eastward one from the North American continent?

Biologists almost unanimously believe that Greenland, in association with several minor islands and the continents of North America and Europe had once formed an integral part of the northern portion of a land mass in geological past. This hypothetical land mass seems to furnish a suitable answer to the question posted above. It is obvious that factually, as their present ranges suggest to us, these species never did emigrate into Greenland, but rather reversely from Greenland, the place that gave them birth, they had migrated to the other parts of the globe. Not improbably they, by the time when the detachment of Greenland actually took place, had already formed their respective areas which

1) Cf. Good, l.c., 224, and in "A Century of Progress in Natural Sciences, 758, Plant Geography (1955). See also Reid, C.: The Relations of the Present Population of the British Isles to the Glacial Period, in Journ. Ecology, 1913, pp. 42-46, wherein the survival of arctic——alpine species is acknowledged (p. 43, paragraph 6).

appear at all events to have surpassed in their extent the imaginary boundaries that once delimited the island from the other parts of the land mass.

Things seem to have been cleared up somehow. Now if we are able to know the age during which the disintegration of that portion of the land mass took place, we are bond to find ourselves not too far in estimating an approximate antiquity of the genus. Unfortunately, matters do not turn out to be as simple as this, for different views had been expressed regarding the date of the disintegration. The question has by now become a reciprocal one in which the logical settlement in our problem may add further testimony to the *pro* and *con* of the rival opinions about the actual time of separation.

Matthew, in the same work referred to above, put the date at the beginning of the Tertiary stage. By Eocene, he states, further inundation by the seas insulated again the continents and islands. Although he acknowledges further communications with intermigrations of mammals between North America and Europe in Oligocene, it is supposed to be by way of "Beringia" rather than through any direct contact by the interposition of Greenland between these continents (pp. 363 & 365). The deep seas between the island and the mainland of Europe had prevented the two from further reunion once separated, but western Greenland is said to come into contact once again with North American .continent for some duration in Miocene.

In contradistinction to the above, we must recall that Limpricht has referred in his discussions to distribution to Arldt's suggestion about the connections between Greenland and Scandinavia through Spitzbergen on the one hand and between Greenland and West Europe through Iceland on the other during Diluvial period.[1] Of course, Limpricht has utilized this view only to account for the presence of the *Pedicularis* species in Greenland, this is because he takes *P. Artselaeri* Maxim[2]. to be the premordial form first generated in the Altai-Tienshan ranges, the alleged cradle of the genus, thus leading to the wrong idea that all species in Greenland are immigrants from the outside world.

Now it becomes an extremely interesting problem to decide which of these two long-spaced geological ages—Cretaceous (or early Eocene) or Pleistocene—is

1) Arldt, T.: Handbuch der Palaeogeographie, I (1910), 591.

2) If *P. Artselaeri* Maxim. and *P. acaulis* Wulf are regarded, on account of their acaulescent habit, as the initiating type of the genus as is supposed by Limpricht and other authors, then, to furnish an adequate answer to the question as to the source or sources from which had arisen such diatypic species in so widely spaced, discontinuous areas would certainly present to these authors a great difficulty.

to be deamed as a more appropriate and reasonable one for the complete severence of Greenland as what we see it to-day, a question which concerns so intimately with the antiquity of *Pedicularis*.

Let us first assume that Greenland was severed from the continents at the dawn of Tertiary as assumed by Matthew. For the very fact that it had detached with all the most primitive forms of *Pedicularis* on it, we cannot but acknowledge that the emergence of these forms must by all intention precede the act of severence, and early Eocene or late Cretaceous should thereby be accepted as the antiquity of the genus, an age, as has been pointed out before, agrees with Limpricht's proposition. Yet for several points of reasoning put forth immediately below, it appears to me to be far too early an age under the point of view of the distribution of *Pedicularis*.

Through fossil remains, we come to know that in Cretaceous, the weather in Greenland was rather warm, so warm that the floristic composition was heavily impregnated with warm temperate colouring[1]. Topographically, relief of the island is devoid of high elevations. It is hard to comprehend how species generated under the condition of a combination of low elevation and genial climate could have survived the glaciation and became ultimately arctic-alpine elements.

We have learnt through our studies in morphology and phylogeny that the lineal descent of various groups and subgroups of *Pedicularis* bears little sign of interruption, and at the same time, the co-existence of the most conservative and the most advanced types side by side with no missing links between the extremities tells us that extinction of species in *Pedicularis* is of very rare occurrence. So it is also difficult to imagine that all through the long geological ages, the evolutionary chains could have remained so thoroughly intact without suffering any indentation to their continuity from the vicissitude of climate and other natural factors.

Again let us see the matter from the standpoint of the stability of species. In biological field, isolation is known to play significant a rôle in the modification[2] and speciation of living beings. Now if the *Pedicularis* species in Greenland had been isolated since the disconnection of the island from the mainland in early Eocene, how are we to interprete the phenomenon that, being separated so long, they could remain so stable without being in the least subjectted to the effect of isolation as the comparison between the populations of these same species on the island and those on the mainlands shows it to be.

1) See Wallace, A. R.: Island Life, p. 116 & 173; Good, 1. c. 268; Wulff, 1. c. 150.

2) The word "modification" is here used in its common, rather than in its genetical, sense.

There is further the vexed problem in the presence on the island of *P. groenlandica* Retz., an elaborately constructed, long-rostrate form. In fact, it is not so much a question as about how it came to be there as about the date of its immigration into the island. It is scarcely doubtful that the species was generated in California or even further south, so Greenland is on the same meridian of distribution as its center of origin. There must have been some meridianal migration that had brought it to the island, a migration which had happened either in a later period when Greenland was reunited with North America after the first separation, or perhaps in the latter part of the same period when Greenland was in union with the continent. We still remember Matthew's proposition about such a reunion in Miocene. As is generally known, Miocene, especially its latter part, is an age which marked the gradual deterioration of climate in the Polar regions. Plant migration, if the general conviction is correct, should have started its southward tide at that time, and we cannot see why *P. groenlandica* Retz. alone should have its migration directed northward against the general current of the migratory tide.

As having been well discussed by Prain, the *Pedicularis* flora has now differentiated into elements which are distinctly marked with constitutional incongruity. By our study in the genus, it has become known that it is not individual species but whole groups or subgroups which reflect their respective biological peculiarities in environmental adaptations. Certain are definitely Arctic-alpine as is characteristically represented by *Rhizophyllum*, while others are manifestly Temperate-intermediate as examplified by *Cladomania*. A remote origin in late Cretaceous or early Eocene seems, too, to be inconsistent with the formation of such constitutionally very incongruous groups.

Now let us see how if Quarternary is taken as the stage when disconnection of Greenland from the continents took place. Upon the acception of such a supposition, an entirely different outlook will at once present itself; each of the several points presented above which brings controversy to Matthew's hypothetical idea will now turn in favour of the latter view. Of course, there is neither the necessity nor the reason for assuming that the date for the separation of Greenland from the continents, especially Europe, was synchronous with or approximate to, the emergence of the genus. Quite possibly, and I believe it to be factually, the first appearance of *Pedicularis* as a genus long antedated the isolation of the island; it might be that, by the time came the displacement, these primitive forms and even certain of their more advanced progenies had already formed areas of considerable extent. But even be it so, the date for the initiation of the genus could not have

been earlier than late Miocene at the most. It is certainly much more easier to convince any one why the continuity in the phylogeny of *Pedicularis* has been so well preserved to this day if its antiquity is not putated as dating back to the remote Cretaceous, but to a much realistic epoch as Miocene or Pleiocene. Similarly, it will give a far more satisfactory answer to the question about the effect of isolation on organisms. Not only because late Tertiary is much more recent in geological scale, but that the narrowing sphere in the condition for existence due to the approaching and the ensuing glacial activities might have served as a brake in cheking any tendency to vary in organic lives, thus rendering the populations of these species on Greenland to remain perfectly stable and to be wholly identical with those on mainlands. At the same time, it also appears more logical that these species, having evolved in a gradually refrigerating climate, were able to survive, later on, the severe glaciations in Pleistocene Epoch.

Finally, there still remains the problem of the existence of constitutionally very different groups within the genus, and the presence of *P. groenlandica* Retz. and other "temperate" species in Greenland and elsewhere within the Arctic Circle. If we take to the notion that the preponderate advance in both evolution and distribution was accomplished in Pleistocene, then there must be close relation between the actions of glaciation and the welfare of the genus. Regarding the Glacial Age, we have the Hypothesis of Alternating Migration, advanced first by Forbes, elaborated later by Darwin and further summarized and discussed in special association with *Pedicularis* by Prain[1]. The basic idea of the hypothesis is founded on the phenomenon of the alternate deterioration and amelioration of climatic conditions known to have happened several times within the relatively short time of Pleistocene Epoch. This hypothesis furnishes fundamentally acceptable answers to both of these two points in question. By its habitually taking to the arctic-alpine environments, *Rhizophyllum* may with good reason be inferred as to have originated at a time when the weather had sufficiently deteriorated in the circumboreal regions, while the preference of a warm, temperate climate of *Cladomania* might have resulted from its emergence, at least certain of its earlier forms, in a time marked by the return of genial weather in one or the other interglacial periods during which the climate is known to have been exceptionally mild, even much warmer than that experienced to-day. The hypothesis also gives an interpretation to the presence of such species as *P. groenlandica* Retz., *P. verticillata* L., *P. Chamissonis* Stev. etc. in the Arctic regions. That they must have accompanied the retreating Arctic-alpine flora in their

1) See Prain, l.c. 40, footnote.

northward migrations, as pointed out by Prain, is a point scarcely open to more debate.

From all the above, it is amply clear that as an age for *Pedicularis*, late Miocene or Pleiocene. is a speculation that captivates the mind far better than Cretaceous or Eocene under biogeographical viewpoint, since it is not only in unison with all critical points found in the distribution of the genus, but also the most accordant with other lines of reasoning.

It now leaves us to consider only the second point, i.e., the chronological orders of the more important subdivisions within the genus. What is significant in this point is the complicated timetable of the various groups and subgroups which shows that neither were their geneses in perfect accordance with their phylogenetic relationships, a feature especially true to the opposite-leaved groups, nor was their subsequent development in proper orders relative to each other.

Regarding the geneses of the groups with alternate phyllotaxy, scarcely any disorder is palpable, but things look very different in their subsequent development. If in their proper orders, it would in the sequence of *Rhizophyllum*, *Sceptrum*, *Apocladus*, *Cladomania* and *Dolichomiscus*. But factually, owing to certain conceivable reasons which we shall refer to presently, the derivative groups *Cladomania* and *Apocladus* actually got an upper hand in producing higher forms in evolutionary scale and in retaining at an earlier date a numerical superiority in species over their parent groups, *Rhizophyllum* and *Sceptrum*. In consequence of such obvious disorder in developmental processes of the alternate-leaved groups, the same was carried into the opposite-leaved domain, and that to a still more appreciable degree. It is not *Dolichophyllum* and *Cyclocladus*, the closest derivate respectively of *Rhizophyllum* and *Sceptrum*, as may be reasonably expected, but phylogenetically the more remote *Orthosiphonia* and *Sigmantha*, that were the groups most early in emergence and most prompt in advancing. Such disorders, like everything else, are written plainly in the distributional patterns.

First, let us examine the behaviours in evolution and migrations of the two leading groups. In *Rhizophyllum*, the most important member is *P. Oederi* Vahl, a seggregate of *P. flammea* L., that had performed the duty of a real progenitor of the group. A comparison of its range in the Arctic with that of the its forebear reveals to us that the species was begotten from the European populations of the latter, since its absence in Greenland and eastern arctic America prevents effectively the formation of a false impression that it was generated elsewhere than Europe. I think that our readers still well remember the fact that, during a long continuum

spent in its migration in Europe and from there eastward through the breadth of Siberia, thence southward to southwestern China where one finds the unfolding of its evolutionary activities in giving birth to angular- and bidentate-tipped forms (*P. pseudoversicolor* H.-M. and *P. habachanensis* Bonati), the species had long remained inert evolutionarily. As may be easily understood, the want in Asia of rather drastic changes in climatic conditions which had served as accelerator to plant migration in Europe and North America must have considerably retarded the paces of dispersion of the species in the former continent.

As regards *Sceptrum*, the first comer, *P. capitata* Adams is just as inactive in evolution as *P. flammea* L. of *Rhizophyllum*. After its zonal dispersal had carried it westward from Greenland to Asia through the landbridge of "Beringia", *P. Sceptrum-carolinum* L. was generated somewhere in Siberia. But for this counterpart of *P. Oederi* Vahl in *Sceptrum*, the area of this group would have been circumscribed definitely to the arctic regions. But exactly like its counterpart, it must have spent a long, long time migrating southward and westward, and its tardy evolution is, too, found in northwestern China where the appearance of the boat-shaped *P. rudis* Maxim. registered the first outburst of higher forms within the group. Such retarded motion in taking evolutionary steps in these oldest groups resulted in the peculiar dispersal phenomenon of their being restricted in range with their more advanced forms to lower latitude at present.

Vivid contrast is to be found in the evolution of *Cladomania* and *Apocladus*. Let us see how matter stands in the former group. We know that the species already referred to above as inhabiting Greenland do not, in fact, include all those present on the island. There are still two more of them, viz., *P. labradorica* Wirsing and *P. lapponica* L. Dissimilar to *P. groenlandica* Retz., these two species have zonal distributions simulating respectively those of *P. Langsdorffii* Fisch. and *P. lanata* Cham. et Schl. The similarity in distributional patterns of these species to the other primitive forms is a sure sign of their being indigenous to Greenland rather than being immigrants as is in the case of *P. groenlandica* Retz. That *P. labradorica* Wirsing is almost surely a bidentate heir to *P. Langsdorffii* Fisch.[1] and *P. lapponica* L. is in turn a rostrate successor to *P. labradorica* Wirsing, thus belonging both to *Cladomania*, discloses to us the hidden relationship in the relative order of development between this derivative group and its parental stocks, namely, by the time Greenland detached from the continents, *Cladomania*, as a secondary

1) Readers may be reminded that *P. Langsdorffii* Fisch. itself was soon improved into a bidentate form, the var. *hians* (Eastw.) Tsoong.

unit, had already advanced to the stages of bidentate and rostrate forms while both *Rhizophyllum* and *Sceptrum* remained, and to a much later age still, in the most primitive "Anodon". Such quickened activity accounts for the wide ranges of ser. *Palustres* and *Racemosae* in all three continents, and the presence of such forms as *P. numudica* Pomel in Algeria, and *P. zeylonica* Benth. and *P. Perrottetii* Benth. respectively in Ceylon and Nilgiri Hills.

In similar manner is the case with *Apocladus*, including both *Eu-apocladus* and *Pseudapocladus*. With such bidentate forms as *P. comosa* L. and *P. sudetica* Willd. widely dispersed in the highest latitudes, these subgroups must also antedate the two leading groups in evolution. Group *Dolichomiscus* is evidently later still than *Apocladus*, as the vicarious *P. acaulis* Wulf and *P. Artselaeri* Maxim. had both arisen from *P. Sceptrum-carolinum* L.; they are from the separate populations of the same species in Europe and Asia that had generated them. In these continents, they both occupy comparatively southerly ranges.

The obvious evolutionary confusion handed down by the alternate-leaved groups to their opposite-leaved derivatives had caused nothing less than a chaos in the chronology of the latter, as it affected, apart from their sequence of development, also the more important sequence of their geneses. When in their normal order, those most affiliated to *Rhizophyllum* and *Sceptrum* as *Dolichophyllum*, *Brachyphyllum* and *Cyclocladus* should be in the van of the array in opposite phyllotaxy, but nothing is so far from the facts. If the present patterns of dispersal do give some information, then it is the less allied *Sigmantha* and *Orthosiphonia* that are the precursors leading the file of the opposite-leaved groups, because they are the only groups in the opposite domain whose constituent species are now to be found in the Circumpolar Province.

The only unit among the more modern groups in opposite phyllotaxy which boasts a slightly longer history is rightfully *Eucyclocladus* whose range has now been extended all along the Himalayan chain by a single species, *P. gracilis* Wall. (subsp. *stricta* Tsoong). The localized distribution of all the remaining groups and subgroups in southwestern China and the Himalayas well demonstrates their late geneses, and these include also *Dolichophyllum* and *Brachyphyllum*, units approaching most closely to *Rhizophyllum*.

From the above, there seems to exist in the geographical distribution of *Pedicularis* certain phenomena which, when taking as a whole, seemingly amount to some form of a "law", and this is shown in the slow but steady evolution and migration of the oldest groups of the genus, the sudden but somewhat erratic

boom in evolution and migration of the groups and subgroups of a secondary nature, symbolized usually by the returning of certain of their members to the highest latitudes, and lastly, the circumscription of the quick-evolving[1], modern units in the southern ranges occupied by the genus.

As to the causation of such phenomena, it seems to involve both intrinsic and extrinsic factors which in most probablity interact very closely each other. In the groups that started the career of the genus, it may be the innate conservatism incident to such ancient, pure-strained units in requisition of more than usual impetus to start their evolutionary activities—impetus which the comparatively monotonous environments in the boreal regions never provide for—that had retarded their proper function in evolution till their arrival at their respective ideal home in the southern latitudes. About the secondary units of presumptive hybrid origin, the accelerated rate of action should be attributed, in my opinion, to heterosis resulted from crossings between phylogenetically remote elements. This promptness in evolution supplied the groups with multiple and diversified forms, which, by the oft-accompanying aggressiveness in such groups, were soon carried far and wide into much broader areas and this was done in far less time than their progenitors.

Can we profit ourselves from the above-revealed complex, almost bewildering, timetable of *Pedicularis*? It shows us that chronology, though almost an integral part of distribution, is an object only attainable with full and accurate marshalling of all knowledges from morphological, phylogenetical and distributional studies. Morphology furnishes, of course, the foundation on which phylogenetic thoughts are based; phylogeny, in turn, leads us to correct ideas about distribution. Chronology, however, is a more intricate problem which, without the coroborative insights into all these three fields, is plainly unimaginable. As an interesting illustration, we may cite *P. Perrottetii* Benth., a somewhat abnormal form having anodontous galea which is yet combined with the longest tube in the genus; and incidentally, it is the only long-tubed species in *Cladomania*. It is almost certain that the last-named characteristic is an inheritance traceable back to the development of the same in *Longiflorae* and *Megalanthae* down the pure line of *Rhizophyllum*. Yet, contrasting the dispersal fact of *Cladomania*, namely, the early emergence of bidentate forms as *P. Langsdorffii* Fisch. var. *hians* Tsoong, *P. labradorica* Wirsing and

1) By quick-evolving, I mean such groups and subgroups which usually achieved their climax of development with a fairly complete series of evolutionary stages in a seemingly comparatively short time, as is shown by the scarcity or complete absence of seggregative forms accompanying the species that represent each one of their evolutionary stages as what are examplified by *Polyschistophyllum* and *Cyathophora*.

the rostrate forms as *P. lapponica* L. and *P. resupinata* L. in the highest latitudes with that of the retarded appearance of the two-toothed ser. *Pseudo-Oederianae* of *Rhizophyllum* in low latitude, it is more than likely that *P. Perrottetii* Benth. long antidated *P. longiflora* Rudolph and its allies in nascency, and it is not wholly improbable that it might even surpass in time of birth the sole bidentate form, *P. habachanensis* Bonati, in the pure line of *Rhizophyllum*. Likewise, the source of the floral structure of the most elaborately constructed members of *Pseudapocladus* in ser. *Surrectae* is to be sought backward to Ser. *Excelsae* of *Eusceptrum*. Yet, *P. groenlandica* Retz. is to be found now in Greenland while *P. Vialii* Franch. and *P. excelsa* Hk. f.[1] are limited in range to Himalayo-Yunnanese Province. Few would doubt, by their respective geographical areas, that *Excelsae* is a morphologically older, but chronologically younger, unit than *Surrectae*. Here the perplexities exhibited in the chronological relationships between the subdivisions within a taxon as low as a genus hint well to us what infinitely more intricacy we may anticipate to find in higher taxonomic taxa as families within the angiosperms. Certainly, the inquisition into the orders of antiquity and evolution of families with morphological characters classifiable to a same level of progress will get results far beyond ordinary expectancy and reasoning.

D. On Prain's projections to the meridians of distribution

Prain, in presenting his meridians of distribution, reasons (p. 45):

"Structure thus directly confirms the evidence from endemic percentage as regards the Japanese, the American and the European meridians of distribution, while curiously reversely, but still equally completely, confirms the evidence from endemic percentage as regards Siberian; whereas along the other three meridians, the percentage of corolla of archaic type gradually falls towards their equatorial limits, along the Siberian meridian, it actually increases. This exceptional arrangement affords on the one hand strong confirmation of the already almost conclusive evidence that the Caucasus is the projection of the Siberian meridian, and on the other makes it almost impossible either that the meridian of distribution for China is derived from that of Siberia, or that the meridian for the Himalaya is extended from that of Caucasus. At the same time there is direct evidence that the meridian of

1) It would be interesting to note how Prain deems *P. excelsa* Hk. f. (p. 44) directly as the "nearest ally" of the species of *Surrectae*. It would surely be a quite logical conclusion but for the fact that there exists no boat-shaped galea along the line of evolution in *Pseudapocladus*; but instead, there is to be found therein the bidentate (ser. *Sudeticae*) and multidentate (*P. maxicana* Zucc.) forms.

Japan is projected in China and extends thence to Himalaya."

That his misinterpretation of the bidentate forms as archaic is the reason for the false increase in the percentage of primitive species in Siberio-Turkestan Province we are now clear. But even the percentage be right as it should be, there will still be serious objection in his fixing definite projections for the various meridians of distribution, as it can be easily proved by the present distribution of the genus. It is but common knowledge that highways of distribution are always open tracks to migrants, and there is no reason why migration can not be reciprocal, unless there is special cause which makes any track a one-way traffic; and this is only in very rare instances as the plant-dispersal shows it to be.

To illustrate this view-point, the dispersal tracks of several groups may be retraced. First of all, there does exist a projection of the Japanese Meridian in China as postulated by him. This is substantiated by *P. tsekouensis* Bonati of Sikang and Yunnan and *P. salviaeflora* Franch. of Yunnan and Szechuan, both of which find their phylogenetic ties in ser. *Gloriosae*, whose center of segregation is in the Japanese Islands. Even more direct evidence is found in group *Sigmantha*. Here *P. ganpinensis* Vaniot of Kweichow and *P. infracta* Maxim. of Japan share between them *P. transmorrissonensis* Hayata of Taiwan Island as their connecting link. What should be noted here is that the communication is apparently bilateral instead of unilateral, because in the former case, the distributional trend is southwestward while in the latter case, the trend is precisely in the opposite direction as the center of origin for *Eusigmantha* is almost without doubt in the northwestern provinces of China Proper.

Yet, the presence of this highway does not mean that it engages all distributional traffics between China and its neighbouring regions. In fact, the greater portion of the *Pedicularis* flora of China and the Himalayas has its sources from the Siberian meridian. To be sure, most of the higher forms in *Sceptrum* are improved descendents of *P. tristis* L., a species whose Siberian origin has never been questioned, and its range has not even been extended to Japan at all. In similar state, the most advanced form in *Neosceptrum*, *P. recurva* Maxim. of Kansu and Sikang is intimately related, if not a direct derivate of *P. proboscidea* Stev. and an indirect descendent of *P. striata* Pall., both of them being inhabitants of Siberia with the latter also common to North China. It is almost inconceivable how with Siberia in close contact, China has to derive all the resources of *Pedicularis* flora from the Japanese meridian.

Prain has also asserted that the Himalayo-Yunnanese Province is a definite

projection of the Tibeto-Chinese. Now let us see wherefrom the *Pedicularis* of the Himalayas were derived. *P. brevirostris* Pennell, a species of ser. *Comosae* found in the western Himalayas and Afghanistan is nearest to, or may even be conspecific with, *P. dolichorrhiza* Schrenk of Siberia and Turkestan. We know that the secondary center of *Comosae* is in the Siberio-Turkestan Province. Japan shares only one species, *P. apodochila* Maxim. with the Island of Saghalin, and possesses in addition a white-floweied form of *P. venusta* Schang., a species ranging from eastern Altai to Kamchatka. On the mainland, the southern-most point touched by the series is northern Chosan, the native land of *P. nigrescens* Nakai. Not a single species is found to the south of this point. Such a situation makes it somewhat fantastic in assuming that the presence of *P. brevirostris* Pennell, as a new segregate of *P. dolichorrhiza* Schrenk, in westeın Himalayas as to have come from Japan by a circuitous route first to Tibeto-Chinese and then to Himalayo-Yunnanese Provinces. The path of migration must have started from Turkestan southward directly through Pamir and Afghanistan to the western Himalayas.

It is equally informative to check the trend of dispersal of group *Orthosiphonia*. The true center of origin of the group, as has been surmised before, is in western Turkestan where *P. pycnantha* Boiss., the real stock of the group, first appeared from *P. Albertii* Regel. On the one hand, this species, taking the same route as *P. brevirostris* Pennell, has now arrived at Kunawar in the western Himalayas, where it is remaining temporarily stable for the time being, as no higher forms had ever arisen here. On the other hand, this same species, in evolving first into ser. *Abrotanifoliae* and then into *Myriophyllae*, issued in North China an active migrant, *P. alaschanica* Maxim., a species, in entering South China, was transformed into subsp. *tibetica* (Maxim.) Tsoong, which has extended still westward to as far as southern Tibet at present. Arising apparently from this fresh stock, the greatly improved members of *Pectinatae* which reach the present zenith in floral construction of the group now come *vis-a-vis* here with their remote ancestor, *P. pycnantha* Boiss. in the western Himalayas. This pincer-like tracks of *Orthosiphonia* aptly disproves the groundless assumption that the source of all *Pedicularis* species in the Himalayas is to be sought in the Yunnan-Sikang area while that of those in the latter area is to be traced far back to the Japanese Archipelago.

So far for the projection of the Japanese meridian. Now let us see how it fairs with the projection of the Siberian merian of distribution in the Caucasian Province. No doubt that *P. pycnantha* Boiss. has its westward extension into the Iranean region, but apparently there is also an eastward counter-flow, though to a

limited extent, of ser. *Caucasicae*, whose representative species is now to be found in northern Iran. But this is not half as important as what we find in the existence of *P. olympica* Boiss. in western Turkey. This species is one of the three constituents of ser. *Limnogenae*, the other two being *P. limnogena* Kern. and *P. recutita* L.[1) These species, being close kins of the members of ser. *Flammeae* and *Hirsutae-verae*, must have rather similar ecological preferances as those of these two series. We know that the physiographic features of the Turano-Iranean regions had so affected the ecological factors that it became wholly unfavourable for such plants of high water-content as *P. Oederi* Vahl, with the consequent absence of this wideranging species in the said region. So, it is plainly impossible to interprete the presence of *P. olympica* Boiss. as coming from the east by the projection of Siberian meridian. To turn our sight westward, we find in the European Province *P. limnogena* Kern. and *P. recutita* L. whose unmistakable relationship reveals to us whence has come *P. olympica* Boiss.

And there is subgroup *Eu-apocladus*, in which the anodontous, comparatively primitive species of ser. *Foliosae* are found in Europe and Asia Minor; only a sole species, *P. sajanensis* Steph. has its home in Siberia. This, combind with the subsequent shift of the center of maximum variation[2) of succeeding bidentate ser. *Comosae* from Europe to eastern Turkestan and Pamir, makes us believe that there is likewise an eastward flow of *Pedicularis* migration from Europe to Siberia[3)

The above-stated thoroughly disproves the validity of such definite projections for the various meridians; and at the same time, with even a greater degree of importance, it shows that the very attempt in their fixation constitutes in itself an example in biological fields of the improper appliance of statistics, which, in spite of the good intention, yields quite wrong results.

E. Physiographic features in relation to the distribution of *Pedicularis*

We have referred already, leading the discussions to all subjects in geographic distribution, to the Theory of Tolerance. The tolerance of a species is of course a complex of ranges in its adaptation to the various phases in environmental conditions, including climatic, edaphic and biotic factors, or in another word, the complex of capacities in withstanding the differences in each and every phase of

1) Cf. observations under ser. *Limnogenae* in the systematic arrangement.

2) About the term "center of maximum variation", more will be debated under the subject of "The area of a species and its relation to evolution".

3) Cf. footnote 2 in page 258.

these conditions. Since the tolerance of a species is chiefly casted by its historical ground, we need feel no surprise in finding close blood relatives and ancestors and offsprings in the same linear descent as those found in the same higher subdivisions of the present genus exhibiting similar preferences in habitate conditions. Only when special conditions come into play do we find manifest changes in the tolerance of a unit during its course of evolution, a phenomenon of not too rare occurrence, but is always clearly discernable whenever it does occur.

Among the factors that control plant distribution, climate has been ranked as of primary importance while the edaphic conditions come as a close second[1]. There is no need to emphasize that these factors must in turn be affected very profoundly by the physiographic features of a given region, large or small, so it follows that these features maintain an indirect, but very important relation with plant dispersal.

The most salient physiographic features in Eurasian continents, serving as the headquarters for *Pedicularis* flora, lie in the elevation in the south of the massive Himalayan-Alpine lines of mountain chains[2] which act as a rainscreen to inland Asia, and the presence of the arid areas and deserts in eastern Mediterranean, Iraq-Iranean regions as a result of the dessication of the former Tethys Sea[3]. The effects of these grandiose physiographic features certainly are sharply reflected in the geographical areas of *Pedicularis* in the two continents.

It is generally conceded that draught exerts a similar, but even more intense effect on plant life than low temperature. So the presence of great stretches of territories of high aridity from eastern Mediterranean to Turano-Iranean regions could not but exercise a profound influence on the distribution of *Pedicularis* on these continents. Clearly there had been created, peradventure through hybridization, groups with special adaptive qualities not possessed by other units of the genus[4]. Of first importance is certainly *Eu-apocladus*, that draught-resisting aggregate of species, which invaded and took up as its domain these arid, *Pedicularis*-vacuum regions referred to above. In later ages, there further arose *Orthosiphonia* with very similar biological peculiarities; and these two units, one alternate- and one opposite-leaved, almost monopolized these areas where conditions are unfavourable to other groups. It will be seen plainly that direct communications of *Pedicularis*

1) Cf. Good, 1. c., p. 361 & sequence.
2) Cf. Babcock, 1. c., pt. I, pp. 93-97; see also Good, 1. c., p. 15.
3) Cf. Babcock, 1. c., p. 100; also Good p. 18.
4) Cf. the view of Kashkarov and Korovin regarding the correlation between plant migration and changes in habitat conditions, as referred to by Wulff, 1. c., 142.

flora between low latitudes of Europe and Asia have since been maintained jointly by these two units, while all intercourses between these two continents effected by the older units as *Eurhizophyllum*, *Eusceptrum* and *Cladomania* were carried out by a circuitous route via Circumpolar Province.[1] The successful invasion of these two groups into the spheres of others both in the warmer Yunnan-Himalayas and the cold Polar regions on the one hand and the complete monopolization of their own domains on the other bespeak aridity to be a more effective barrier

---

1) Babcock, in discussing the distribution of genus *Crepis*, relates (p. 102) to Engler's appreciation of the importance about a southwesterly trend of Asiatic-European plant migration and his three generalizations about the development of the high montane flora before, during and after the glacial period. Three species, namely, *Aconitum Anthora*, *Saussurea discolor* and *Pedicularis comosa*, are named as the representatives of a number of plants whose distribution is characterized in common by their presence in Altai, Caucasus and Alps on the one hand and an absence in Scandinavia on the other. Such peculiar dispersal is supposed to give proof to an assumption that their presence in Europe was through a southwesterly plant migration from Altai to the Alps.

From our arguments given above and in relation to Prain's projection of the Siberian meridian of distribution (p. 254 et seq.), there is not the slightest doubt that the trend of migration, at least that of *P. comosa* L., is diametrically opposed to that assume by Engler. It is true that this species is absent from Scandinavia as asserted, but this does not necessarily mean that it owes its presence in the Caucasus and Europe to a southwesterly extension from Altai.

We have already presented, in respect to the center of origin of the genus (check the discussions in pp. 68 & 69 in the second issue of this paper), the fact that in Altai, there is to be found only one alternate-leaved group other than the one in question (*Eu-apocladus*). Now, *P. Oederi* Vahl and its seggregate, *P. Albertii* Regel, are the two representatives of the former unit found in Altai, and it is singularly impossible to generate a contention that the latter group could have arisen out of these species here. Besides, the inreversible positions occupied by the center of origin of the anodontous *Foliosae* and the bidentate *Comosae* in the Balkans and Alps and by the secondary center of the latter series in eastern Turkestan add further difficulty in assuming that *P. comosa* L. has a trend of migration in a southwesterly direction.

To put the matter under the general view-point of plant distribution and evolution, glaciatious, though having exterminated by their catastrophic disturbances a countless number of species wherever they extended, might, on the contrary, have also incited with their tremendous pressure exerted incessantly at the heels of migrating floras, the genesis of new forms adaptive to environments originally unsuitable to their ancestors—forms, which but for such extraordinary pressure, would have never been generated. This seems to be clearly recorded in the distributional patterns of Eurasian *Pedicularis*.

As having been referred to before, what little glaciation Asia possesed is utterly incomparable to that of Europe. With the great expanse of territories in high aridity in the west as an effective barrier, the components of eastern Asiatic *Pedicularis*, being easy-going without the interference of glaciation, did not at all generate forms that are truly draught-resisting, and the extension of their areas to Europe was not by taking a shortcut in a southwesterly trend, but rather through a round-about way northward investing first Siberia and then westward to Europe. It is most characteristically examplified by *P. verticillata* L. of *Eusigmantha*. Obviously not so with the European *Pedicularis*. Hard pressed by the ever-encrouching ice caps from the north and the glaciers of the Alps, new forms that could withstand aridity arose, by compulsion, out of the old, arctic-alpine stocks and these forms were not slow to invade the territories open to them in the east. This, I believe, is the reason why such particular unti as *Eu-apocladus* was originated. So, in as much as *Pedicularis* is concerned, there is really no perfect trend of migration from Altai to the Balkans to be found; rather, it is the reverse that is true.

to plant dispersal than low temperature.

Of less magnitude yet perhaps of more interest are the phenomena in the distribution of *Pedicularis* in the eastern and western sections of the great Himalayas. The difference in physiographic and natural aspects of the two sections of this huge mountain range are well-known[1]. and it leaves for us only to check the dispersal behaviours of *Pedicularis* in response to these differences. Here strong contrast is to be found in the distribution of the two constitutionally very different units, the moisture-loving or almost helophytic *Eurhizophyllum* and the xerophytic *Orthosiphonia*. The former, with its climax in floral development attained already by *Longiflorae* and *Megalanthae* in the eastern section of the range shows an apparent anticlimax in the western section. In the former series, only the yellow-flowered *P. longiflora* Rudolph] (var. *tubiformis* Tsoong) has extended further westward from Nepal Himalaya. The two other species that only occur in the west are *P. Hookeriana* Wall. and *P. punctata* Decsne., forms which have manifestly shorter corolla-tube than their apparent relative, the eastern *P. siphonantha* Don. In the latter series, similar conditions exist. The species inhabiting the western section are *P. bicornuta* Klotsch., *P. elephantoides* Benth. and *P. Hoffmeisteri* Klotsch. Their blood relatives in the eastern section are *P. megalochila* Li, *P. megalantha* Don and *P. pauciflora* Pennell. Both as regards floral structure and coloration, the eastern species are admittedly more advanced than the western forms. Evidently, *P. megalochila* Li which inhabits southeastern Tibet is a polychromic species, but *P. megalantha* Don and *P. pauciflora* Pennel are red-flowered. On the other hand, all the western species are yellow-flowered. In floral structure, only *P. Hoffmeisteri* Klotsch. can be said as a close match to *P. megalantha* Don, while the other two species have decidedly less specialized lower lips. In the latter group, *Orthosiphoina*, precisely the reverse prevails. No highly improved form is seen among the several species, mostly "Anondon", in the eastern Himalayas, save two, the longer-beaked *P. Oliveriana* Prain and the moderately beaked *P. alaschanica* Maxim. (subsp. *tibetica* Tsoong), the latter being the apparent ancestor of the advanced forms in the western section, wherein are to be found quite a number of its derivates with elaborate corollal structures belonging to ser. *Pectinatae*.

From the foregoing, it is easily perceivable that the adaptation to grand scale

1) See Pennell, F. W.: The Scrophulariaceae of western Himalayas (Monogr. V, Acad. Nat. Sci. Philad., 1943), p. 2, and the footnote therein. In the footnote, comparisons between species of *Pedicularis* in the two sections are made, but no mention is made about their affinities. It is also informative to consult "Vegetation of the Himalayas" by Joshi, A. C., in March of India, v (1952), pp. 54-58.

environmental peculiarities as a result of major physiographic aspects is often fulfilled, not by a single species, but rather by a collection of species which repiesents a whole phyletic descent. So, to a taxonomist in quest of a natural system, it is even more meaningful to take care of the tolerance collectively on a group, rather than on a specific, basis.

F. Altitudinal distribution of *Pedicularis*

Twice have we referred to the Theory of Tolerance and its important bearing on phytogeography. Here we are going to find out its relation with the altitudinal distribution. It is practically impossible to learn exactly what an abstraction of complex nature as the tolerance of a plant really is, even though analysis of the diverse factors in connection with its habitation is critically made[1]. But since tolerance is manifested in the adaptation or preference of certain particular ecological environment on the part of the plant, then, without making undue effort, we may take the said environment as a manifestation, in general, of its tolerance[2].

It is but common knowledge that altitude is only latitude in a vertical, but very much abbreviated, order. In such brief order, one would naturally find things changing in short orders too. Included in the things changing, there must be, first of all, rapid changes in climatic conditions——that primary factor governing plant distribution as has already been alluded to before; and with it, there would be further concurrent changes in edaphic and biotic conditions as well. This is the reason why we are accustomed to see control over distribution by altitude has ever been manifested in the maintainance of sharp vegetational belts on high mountains. So here, the altitudinal limits for a species may at least be regarded as an indication of its tolerance in that pre-eminent phase of ecology, i.e., the climatic factor.

With respect to the connection between the formation of tolerance of any given species and its manifestation as a specific altitudinal preference, especially in a genus like *Pedicularis*, the following interpretation may be given: if a species was originated in high latitude under refrigerating climatic conditions, we may well anticipate it, when coming down to lower latitudes, to take by preference high altitudes where is to be found a climate somehow approaching the original; conversely, if a species had made its appearance at a time when the weather was comparatively mild as

1) Cf. discussions under "The environment is holocoenotic", in Cain, S. A.: Foundation of Plant Geography (1944), 16.

2) It is quite within expectation that there is to be experienced great difficulty in comparing the fine results of ecological research to the coarse studies in distribution. Cf. Cain, l. c., p. 7, paragraph 2.

during certain inteıglacial equilibrium, it would naturally, in migrating southward, took, through the influence of its tolerance, regularly to lower altitudes where the climate must suit it better. As to the relationship of tolerance of a single species and that of a collection of species, there is no need to say anything more, as it has been discussed fully in the foregoing subjects.

In the past works on *Pedicularis*, little attention has been paid to this particular item of plant geography, in which, however, we may hope to find something not obtainable from other lines of distributional studies. What is written therein offers little else than figures showing a certain number of species to be found at certain elevations. For the special purpose of using it as a medium for checking the triple correlations of this particular phase of distribution towards the evolution, the migration and the system of the genus, a table showing elevations as frequented by species of various groups and subgroups in systematic sequence is presented below. After each species, a set of two figures is given, the left-hand figure representing the lower, and the right-hand one the upper perpendicular limit of the species. When only a single datum is available in a species, then it is recorded twice to give the table its necessary balance. It must be noted here that I do not claim the table to be an exhaustive one; it is, in fact, far from being so. I have not troubled myself to go to any great length in collecting all available data, knowing very well that this certainly will not in the least impair the value of our statistics in their intended purpose. For the sake of easier comparison, a second table containing the mean of respective upper and lower limits for the groups and subgroups has been separately supplied.

Table showing upper and lower altitudihal limits of species arranged in systematic sequence (in meters)

Grex RHIZOPHYLLUM	
Subgrex EURHIZOPHYLLUM	
Ser. Flammeae	
P. flammea L.	50–750
P. Oederi Vahl	300–5100
P. angustiflora Limpr. f.	3960–5335
P. orthocoryne Li	4420–4880
Ser. Corydaloides	
P. cryptantha Marq. et Shaw	2600–3600
P. corydaloides H.-M.	3200–3800

Ser. Pseudo-oederianae	
P. pseudoversicolor H.-M.	3600–4700
P. habachanensis Bonati	4100–4200
Ser. Rhynchodontae	
P. rhynchodonta Bur. et Fr.	3660–4700
Ser. Filiculae	
P. filicula Franch.	2800–4800
P. Lecomtei Bonati	3500–3500
Ser. Macrorhynchae	
P. macrorhyncha Li	3660–3660
Ser. Robustae	
P. Daltonii Prain	4200–5100
P. nepalensis Prain	3900–4200
P. robusta Hk. f.	4800–4800
Ser. Macranthae	
P. insignis Bonati	4200–4300
P. Klotzschii Hurus.	3600–4500
P. Scullyana Prain	3300–3600
Ser. Pumilliones	
P. bella Hk. f.	4880–4880
P. Przewalskii Maxim.	4000–4830
Ser. Longiflorae	
P. longiflora Rudolph	3350–5300
P. chinensis Maxim.	1700–2900
P. armata Maxim.	3000–4600
P. Garnierii Bonati	3000–3600
P. cranolopha Maxim.	2700–4000
P. humilis Bonati	3050–3050
P. Hookeriana Wall.	2700–4500
P. punctata Decsne.	2500–4500
P. variegata Li	4150–4150
P. siphonantha Don	2800–5000
P. tenuituba Li	3080–3080
P. Paxiana Limpr. f.	4300–4300
P. dolichantha Bonati	3200–3200
P. latituba Bonati	3080–3080
P. sigmoidea Franch.	3000–3600
Ser. Megalanthae	

P. bicornuta Klotz.	2800–5100
P. elephantoides Benth.	2600–3400
P. megalantha Don	2100–4300
Subgrex RHIZOPHYLLIASTRUM	
Ser. Roseae	
P. muscoides Li	3690–5335
Ser. Merrillianae	
P. Merrilliana Li	3250–4900
P. pulchella Pennell	3000–3150
Ser. Asplenifoliae	
P. longipedicellata Tsoong	4700–4700
P. Meyana H.-M.	3660–4500
P. Yui Li	4100–4100
P. tsarungensis Li	4000–4000
Ser. Paucifoliatae	
P. micrantha Li	3100–3100
P. yunnanensis Franch.	3050–4000
P. Forrestiana Bonati	3350–4000
P. microcalyx. Hk. f.	3900–4050
Ser. Mychophilae	
P. mychophila Marq. et Shaw	4000–4900
Ser. Franchetianae	
P. Franchetiana Maxim.	3660–4900
Ser. Pseudomacranthae	
P. aschistorhyncha Marq. et Shaw	3400–3600
P. Fletcherii Tsoong	2900–3900
Ser. Albiflorae	
P. Regeliana Prain	3300–3900
P. rhizomatosa Tsoong	3650–3650
P. perpusilla Tsoong	3600–3600
P. Hicksii Tsoong	4350–4350
P. tapaoensis Tsoong	4700–4700
P. Tayloriana Tsoong	4100–4100
Ser. Neolatitubae	
P. neolatituba Tsoong	4700–4700

Grex DOLICHOPHYLLUM

Subgrex EUDOLICHOPHYLLUM

Ser. Cernuae

P. cernua Bonati 3800–4200

Ser. Pseudorostratae

P. chenocephala Diels 3660–4300

P. tatsienensis Franch. 4100–4420

Subgrex DOLICHOSTACHYS

Ser. Pilostachyae

P. pilostachya Mixim. 4720–5070

P. ternata Maxim. 3200–4550

Ser. Tantalorhynchae

P. tantalorhyncha Franch. 3050–4000

P. tantalorhynchoides Tsoong 4200–4200

Ser. Meteororhynchae

P. meteororhyncha Li 4150–4150

Grex BRACHYPHYLLUM

Subgrex EUBRACHYPHYLLUM

Ser. Lyratae

P. stenocorys Franch. 3100–3900

P. cymbalaria Bonati 3400–4400

P. deltoidea Franch. 3200–4200

P. lyrata Prain 4000–4200

P. polyodonta Li 2320–3225

P. lutescens Franch. 3500–4000

Ser. Brevifoliae

P. brevifolia Don 3000–3600

P. alopecuros Franch. 2300–4000

P. porrecta Wall. 3900–4500

P. verbenaefolia Franch. 3300–4000

P. Smithiana Bonati 3350–4000

P. Tsaii Li 4000–4250

Ser. Debiles

P. Poluninii Tsoong 4400–4400

P. debilis Franch. 2750–2750

P. confertiflora Prain 3850–4850

P. sphaerantha Tsoong 3850–4100

P. tenuicaulis Prain 3950–3950

P. Maxonii Bonati 3000–3000

P. canescens Tsoong 4650–4900

P. lamioides H.-M.	3400-4150
P. instar Prain	3600-3900
Ser. Intergrifoliae	
P. integrifolia Hk. f.	2700-4200
Subgrex BRACHYPHYLLIASTRUM	
Ser. Binariae	
P. binaria Maxim.	3900-4000
Ser. Urceolatae	
P. urceolata Tsoong	3800-3800
P. xylopoda Tsoong	4650-4900
Grex APOCLADUS	
Subgrex EU-APOCLADUS	
Ser. Foliosae	
P. Wilhelmsiana Fisch.	1500-2290
P. condensata M. Bieb.	2121-2124
P. atropurpurea Nordm.	2121-2121
Ser. Comosae	
P. heterodonta Panc	1300-1300
P. comosa Linn.	1242-2727
P. petiolaris Tenore	2100-2100
P. Ferdinandii Bornm.	2050-2300
P. uliginosa Bunge	3800-4000
P. graeca Bunge	1680-1830
P. leucodon Griseb.	1525-2140
P. physocalyx Bunge	
var *dubia* Bonati	3000-3000
P. achilleaefolia Steph.	4000-4000
P. dolichorrhiza Schrenk	3050-4000
P. gyroflexa Vill.	1500-1500
P. elegans Ten.	2000-2800
P. caespitosa Sieber	1200-2500
P. rostrata Linn.	1200-2300
P. pyrenaica Gay	2000-2200
P. mixta Gren. et Godr.	2000-2200
P. Nordmanniana Bunge	2300-2500
Ser. Strobilaceae	
P. gracilicaulis Li	3000-3300

P. strobilacea Franch.	3050–3960
P. dichrocephala H.-M.	3350–3450
Ser. Oliganthae	
P. tahaiensis Bonati	2200–3200
P. cephalantha Franch.	3350–4850
var. *szetchuanica* Bonati	2800–4500
P. longipetiolata Franch.	2800–3600
P. oligantha Franch.	3000–3000
P. tachanensis Bonati	2200–2200
Ser. Oxycarpae	
P. Monbeigiana Bonati	3000–4200
var. *birmanica* Bonati	3000–3000
P. Stewardii Li	2200–2200
P. tibetica Franch.	4100–4100
P. torta Maxim.	2500–4000
P. Davidii Franch.	2250–3800
Ser. Amplitubae	
P. amplituba Li	3460–3460
Ser. Rhinanthoides	
P. rhinanthoides Schrenk subsp. *typica* Pennell	3000–4000
var. *labellata* Prain	2750–5500
var. *tibetica* Bonati	3000–5000
Subgrex PSEUDAPOCLADUS	
Ser. Compactae	
P. Orizabae Cham.	3000-4000
P. Parryi Gray	4000-4000
P. mexicana Zucc.	1800-2200
P. similis Heller	2750-2750
P. incarnata Jacq.	1200-2300
Ser. Incurvae	
P. incurva Benth.	3200-4200
Ser. Surrectae	
P. attollens A. Gray	1830-3050
Grex ORTHOSIPHONIA	
Ser. Caucasicae	
P. pycnantha Boiss.	2700-5100
P. caucasica M. Bieb.	4000-4100

P. cadmea Boiss.	1880-3050
Ser. Molles	
P. mollis Wall.	3000-4500
Ser. Gibberae	
P. gibbera Prain	3600-4200
Ser. Denudatae	
P. polygaloides Hk. f.	3900-4200
P. denudata Hk. f.	3600-3900
Ser. Abrotanifoliae	
P. obscura Bonati	3660-4270
P. densispica Franch.	1880-4270
P. brevilabris Franch.	3500-3500
Ser. Platyrhynchae	
P. pulchra Pauls.	4000-4000
P. chorgossica Regel ex Maxim.	1525-1830
Ser. Myriophyllae	
P. subrostrata C. A. Meyer	2100-2300
P. myriophylla Pall. var. *tatarinowii* Maxim.	2100-2300
P. alaschanica Maxim.	1750-3250
P. Chamissonis Stev. var. *japonica* Miq.	1500-3000
P. scolopax Maxim.	3500-4000
P. cristatella Pennell et Li	2580-2750
Ser. Pectinatae	
P. tenuirostris Benth.	2300-3700
P. pectinata Wall.	2100-4400
P. Stewartii Pennell	2400-3700
P. rhynchotricha Tsoong	3700-3900
P. cyrtorhyncha Pennell	2000-4300
P. pyramidata Royle	2700-5000
subsp. *kashmiriana* Tsoong	2000-4500
subsp. *multiflora* Tsoong	1700-2600
Ser. Gyrorhynchae	
P. gyrorhyncha Franch.	2750-3350
P. Wangii Li	2700-3600
P. Duclouxii Bonati	3400-4300
Ser. Semitortae	
P. Oliveriana Prain	3600-4300
P. semitorta Maxim.	2500-3500

Grex SIGMANTHA	
Subgrex NOTHOSIGMANTHA	
Ser. Cheilanthifoliae	
P. cheilanthifolia Schrenk	3300-4900
P. ophiocephala Maxim.	3400-5100
P. globifera Hk. f	3350-4500
Ser. Curvitubae	
P. anas Maxim.	3000-3900
Subgrex EUSIGMANTHA	
Ser. Plicatae	
P. plicata Maxim.	2900-3500
P. luteola Li	3660-3660
Ser. Verticillatae	
P. rupicola Franch.	2745-4800
P. Roylei Maxim.	3300-5000
P. Shawii Tsoong	4500-4500
P. nana C. E. C. Fisch.	4000-4920
P. anthemifolia Fisch.	2000-2500
P. violascens Schrenk	4000-4300
P. nodosa Pennell	5000-5000
P. Chingii Bonati	3000-4200
P. kansuensis Maxim.	1825-3850
P. szetschuanica Maxim.	4450-4550
P. involucrata Tsoong	3300-3600
P. dolichostachya Li	3660-3660
P. diffusa Prain	3300-3900
P. stenotheca Tsoong	3950-3950
P. verticillata Linn.	2100-3350
P. tangutica Bonati	1380-2500
P. refracta Maxim.	1300-1300
P. brachycrania Li	3700-3700
P. likiangensis Franch.	3200-4600
P. lineata Franch.	2800-4570
P. holocalyx H.-M.	2000-2000
P. spicata Pall.	1500-2500
P. Taquetii Tsoong	1700-1800
Ser. Microchilae	
P. microchila Franch.	2750-4000

Subgrex RIGIOCAULUS

Ser. Salicifoliae

P. salicifolia Bonati	900-3500

Ser. Rigidae

P. comptoniaefolia Franch.	2400-3000
P. rigida Franch.	2500-3000
P. Mairei Bonati	2500-2600

Grex CLADOMANIA

Ser. Hirsutae-centripetae

P. Langsdorffii Fisch.	170-500

Ser. Canadenses

P. canadensis Linn.	1600-3200
P. crenulata Benth.	2300-2450

Ser. Palustres

P. sylvatica Linn.	90-300
P. lusitanica Conth.	600-1200
P. numudica Pomel	20-120
P. palustris Linn.	370-370
P. labradorica Wirsing	130-900

Ser. Racemosae

P. lapponica Linn.	7-1200
P. resupinata Linn.	300-1600
P. racemosa Douglas	30-2200

Ser. Carnosae

P. nigra Bonati	1100-2100
P. Collettii Prain	1200-1500
P. corymbosa Prain	1200-1200
P. veronicifolia Franch.	1600-2600
P. kouytchenensis Bonati	2800-3350
P. Tsiangii Li	466-466
P. crenata Maxim.	3350-3350
P. zeylonica Benth.	1800-2100
P. bifida Pennell	900-2100

Ser. Microphyllae

P. tenuisecta Franch.	1500-3660
P. Henryi Maxim.	400-1420
P. Labordei Vaniot	130-2500

Ser. Polyphyllatae	
P. Stadlmanniana Bonati	2440–3050
P. kariensis Bonati	3960–3960
P. pinetorum H.-M.	2500–2800
P. Limprechtiana H.-M.	2100–3400
P. gruina Franch.	2600–3000
P. polyphylloides Bonati	3300–3400
Ser. Furfuraceae	
P. Hemsleyana Prain	2900–4000
P. furfuracea Wall.	2400–3600
P. Pantlingii Prain	3500–4200
P. taliensis Bonati	2750–3350
Grex CYATHOPHORA	
Ser. Reges	
P. rex C.B. Clarke	2500–4300
P. Lipskyana Bonati	1930–3800
P. thamnophila Li	3200–3500
P. cupuliformis Li	4000–4000
Ser. Cyathophylloides	
P. cyathophylloides Limpr. f.	3850–3850
Ser. Superbae	
P. superba Maxim.	2800–3900
Ser. Cyathophyllae	
P. connata Li	4150–4150
P. cyathophylla Franch.	4700–4700
Grex DOLICHOMISCUS	
Subgrex PTERIDIOIDES	
Ser. Pteridifoliae	
P. pteridifolia Bonati	800–1600
Ser. Phaceliaefoliae	
P. phaceliaefolia Franch.	1600–1850
P. Fargesii Franch.	1400–3800
Subgrex EUDOLICHOMISCUS	
Ser. Acaules	
P. artselaeri Maxim.	1100–1500
Ser. Vagantes	

P. vagans Hemsl.	950-2200
Ser. Longipedes	
P. nasturtiifolia Franch.	2000-2000
P. longipes Maxim.	4100-4100
P. axillaris Franch.	2750-3350
P. filicifolia Hemsl.	2500-3200
Ser. Omiianae	
P. omiiana Bonati	2300-3200
Ser. Muscicolae	
P. macrosiphon Franch.	1200-3500
P. geosiphon Smith et Tsoong	3500-3900
P. muscicola Maxim.	1750-2650
Grex CYCLOCLADUS	
Subgrex EUCYCLOCLADUS	
Ser. Salviaeflorae	
P. salviaeflora Franch.	2000-3900
Ser. Melampyriflorae	
P. floribunda Franch.	2700-2700
P. melampyriflora Franch.	2700-3600
P. pseudomelampyriflora Bonati	3050-3050
Ser. Longicaules	
P. longicaulis Franch.	3660-3880
P. Dielsiana Bonati	2135-2135
Ser. Graciles	
P. gracilis Wall.	1800-3900
P. khasiana Pennell	1200-1900
Grex NEOSCEPTRUM	
Subgrex EUNEOSCEPTRUM	
Ser. Striatae	
P. striata Pall.	1300-2990
P. Grayi A. Nelson	2600-2800
P. mandshurica Maxim.	1205-1205
Ser. Recurvae	
P. recurva Maxim.	3250-3600
Grex SCEPTRUM	
Subgrex EUSCEPTRUM	

Ser. Gloriosae	
P. Sceptrum-carolinum Linn.	400–500
Ser. Grandiflorae	
P. grandiflora Fisch.	350–400
Ser. Tsekouenses	
P. tsekouensis Bonati	3050–4200
Ser. Tristes	
P. shansiensis Tsoong	1400–1800
P. tristis Linn.	2750–3050
Ser. Galeatae	
P. galeata Bonati	4000–4270
Ser. Rudes	
P. Fischeriana Tsoong[1]	3333–3333
P. rudis Maxim.	2350–3350
P. princeps Franch.	2800–3370
P. Dunneana Bonati	2440–4000
Ser. Imbricatae	
P. Clarkei Hk. f.	3600–4500
P. platychila Tsoong	4600–4600
P. mucronulata Tsoong	2600–2600
P. imbricata Tsoong	4600–4600
Ser. Dolichocymbae	
P. dolichocymba H.-M.	3500–4300
Ser. Ingentes	
P. pseudosteiningeri Bonati	3000–4300
P. trichocymba Li	2745–4730
P. ingens Maxim.	3050–3900
Ser. Trichoglossae	
P. trichoglossa Hk. f.	3600–5000
P. rhodotricha Maxim.	3660–4000
Ser. Lasiophrydes	
P. craspedotricha Maxim.	3400–4500
P. lasiophrys Maxim.	3400–4750
P. cinerescens Franch.	4000–4400
Ser. Kongboenses	
P. kongboensis Tsoong	4000–4000
P. retingensis Tsoong	4200–4200

1) See note under this name to be published in the systematic treatment.

Ser. Excelsae

P. Vialii Franch.	2700–3600
P. excelsa Hk. f.	3600–3600

Ser. Kialenses

P. kialensis Franch.	3050–4875

Table showing the means of the lower and upper limits for the various groups and subgroups (in meters)

Grex RHIZOPHYLLUM	
Subgrex EURHIZOPHYLLUM	3206–4128
Subgrex RHIZOPHYLLIASTRUM	3735–4188
Grex DOLICHOPHYLLUM	
Subgrex EUDOLICHOPHYLLUM	3853–4306
Subgrex DOLICHOSTACHYS	3864–4394
Grex BRACHYPHYLLUM	
Subgrex EUBRACHYPHYLLUM	3433–4022
Subgrex BRACHYPHYLLIASTRUM	4116–4233
Grex APOCLADUS	
Subgrex EU-APOCLADUS	2479–3109
Subgrex PSEUDAPOCLADUS	2540–3214
Grex ORTHOSIPHONIA	2730–3731
Grex SIGMANTHA	
Subgrex NOTHOSIGMANTHA	3263–4600
Subgrex EUSIGMANTHA	3001–3700
Subgrex RIGIOCAULUS	2075–3025
Grex CLADOMANIA	1531–2277
Grex CYATHOPHORA	3766–4025
Grex DOLICHOMISCUS	
Subgrex PTERIDIOIDES	1267–2417
Subgrex EUDOLICHOMISCUS	2215–2960
Grex CYCLOCLADUS	
Subgrex EUCYCLOCLADUS	2406–3133
Grex NEOSCEPTRUM	
Subgrex EUNEOSCEPTRUM	2088–2648
Grex SCEPTRUM	
Subgrex EUSCEPTRUM	3077–3740

Now let us have an examination of the above tabulations. The first step should be a comparison between the elevations occupied by the two representative groups, *Rhizophyllum* and *Sceptrum*.

We see in the second table the sets of figures after subgroups *Eurhizophyllum* and *Eusceptrum* to be respectively 3,206-4,128 m. and 3,077-3,740 m. Superficially, these figures show that, as a true arctic-alpine unit, *Rhizophyllum* takes toelevations which by comparison are not eminently higher than those frequented by *Sceptrum*. But we must not be deceived by these figures, because upon scrutinization, it has been found that certain factors have introduced modifications which conceal the true aspect in the altitudinal dispersal of these groups.

To find out these factors, the first table showing elevations for the individual species should be consulted. Under subgroup *Eurhizophyllum*, there are listed two species which are found to inhabit extremely low elevations, namely, *P. flammea* L. and *P. Oederi* Vahl, with their sets of figures showing 50-750 m. and 300-5,100 m. respectively. The outstanding feature in these figures lie in that the difference between the extremes for the former is only 700 m., while that for the latter rises abruptly to 4,800 m. Here the difference is indeed striking enough, but there is really nothing incomprehensible about this phenomenon if a comparison between these figures and the geographical areas of these species is made. We know that the former is a species restricted to arctic and subarctic regions while the latter has now extended its area far southward to the Alps in the west and the Himalayas in the east. Such facts can only mean that *P. Oederi* Vahl., acting as the true ancestor to all higher forms of *Rhizophyllum*, has shown at almost the very beginning of the group a strong predilection of arctic-alpine climate by taking higher and higher elevations after leaving its center of origin in the Circumpolar Province. Here such extremely low figures for the Polar species, though easily blending themselves imperceptibly with the others if ever found in low elevation units, would certainly make themselves the prominent features of, and at the same time, tend to lower the mean figures for, a group of alpine nature as *Rhizophyllum*.

In the same subgroup, most constituents prefer the highest altitude as *P. Oederi* Vahl does, and a total of five species among them are encountered at elevations over 5,000 m., a number unexcelled by any other group within the genus. These facts tell us that *Eurhizophyllum* as a unit adapts particularly to frigid alpine life. Yet there are in our table altogether seven species that come down to below 3,000 m. altitude; they are *P. filicula* Franch., *P. chinensis* Maxim.,

P. siphonantha Don, *P. cranolopha* Maxim., *P. bicornuta* Klotch., *P. elephantoides* Benth. and *P. megalantha* Don. Of the seven, *P. filicula* Franch. does not come down much lower than 3,000 m. and its upper limit is still near 5,000 m. mark. The remaining six species invade much lower elevations, among which *P. chinensis* Maxim. and *P. megalantha* Don descend to the lowest altitude, being found at 1,700 m. in the North China hills and 2,100 m. on the southern slope of eastern Himalayas respectively. This phenomenon discloses to us a definite tendency to come down to lower altitude in among the advanced forms of *Eurhizophyllum*. Apparently this tendency has already set in but not quite noticeable in *Filiculae*, as the series is yet not very distant from *Flammeae* in evolutionary scale, but becomes distinctly so in *Longiflorae* and *Megalanthae*, two series which represent the apogee in the evolution of the subgroup at present. Here is another factor which helps lessoning the mean value of altitudinal figures for *Eurhizophyllum*.[1)]

Shifting our attention to *Eusceptrum*, the species of the initiating ser. *Gloriosae* and the closely linked *Grandiflorae* are found to be low-land plants below 500 m. altitude. In ser. *Tristes*, the elevations occupied by the two species cited are already slightly higher, their figures being 1,400 m. and 3,050 m. respectively for the lower and upper limits as occupied by *P. shansiensis* Tsoong and *P. tristis* L. From here on, the perpendicular positions for the component species of the various series become increasingly, though somewhat erratically, higher until the subgroup comes to *Lasiophrydes* and *Kongboenses* where an extraordinary high mark of 6,000 m. is touched by *P. lasiophrys* Maxim., while the average also reaches well above 4,000 m. This being so, that there is also a tendency on the part of *Eusceptrum* in changing the altitudinal partiality is obvious enough, although the change here takes apparently a reverse order to *Rhizophyllum*. The early appearance in *Eusceptrum* of this tendency greatly elevates the figures in its vertical distribution; this, in combination with the reverse tendency in its opponent subgroup, makes the figures of these two units almost one equalling to the other. Obviously, at their respective initial end, the two representative units differ markedly, at least so far as their altitudinal preferences are concerned, yet as their constituents invaded new territories, the contact of fresh environments first started and then quickened their paces of evolution, and with it came the gradual changes to their original

1) To prove the matter in another way, we may have a look at the figures under subgroup ***Rhizophylliastrum***, the branch of ***Rhizophyllum*** originated and developed exclusively in low latitude. Here, with the absence of the low-elevation, arctic forms and the lack of tendency in lowering its altitudinal distribution, the figures of this subgroup show therefore a much higher value than those of ***Eurhizophyllum***.

tolerances, a process very well reflected in the corresponding adaptations to altitude in the new forms resulted. What is even more interesting is for us to detect again at the terminus of the evolutionary trend in present-day *Eusceptrum* two advanced forms, namely, *P. Vialii* Franch. and *P. excelsa* Hk. f., inhabiting elevations much lower than those less specialized species of ser. *Trichoglossae*, *Lasiophrydes* and *Kongboenses*, a clear sign of a second shift in direction after reaching the upper limit in ascent.

Now let us inspect those secondary groups and subgroups. In the second table, we find the set of figures under the opposite-leaved *Eudolichophyllum*, a unit predominently influenced by *Flammea*-type, to be higher even than those of *Eurhizophyllum*, being 3,853-4,306 m. These figures would surely approach very nearly those of the latter unit, if a deduction of its low altitude species is made. Contrary to the foregoing, the sets of figures under those groups and subgroups eminently influenced by *Capitata*-type like *Dolichomiscus*, *Cyclocladus* and *Neosceptrum* show the elevation values to be much lower, with their lower limit at 1,267 m., the figure found under subgroup *Pteridioides*, and their upper limit at 2,648 m., as denoted by subgroup *Euneosceptrum*.

In the less commitible and indirectly originated groups, we find the mean under *Eu-apocladus*, *Orthosiphonia* and *Cladomania* in sets of figures of 2,479-3,109 m., 2,730-3,731 m. and 1,531-2,277 m. respectively. It is almost superfluous to point out here that the two former groups with higher figures approach closer to *Rhizophyllum* while the last one with the lowest figure stands nearer to *Sceptrum*. Even inside a single unit like *Sigmantha*, what it manifests is almost a complete repitetion of the above cases. Here, the set of figures for the possibly *Orthosiphonia*-derived *Nothosigmantha* is 3,263-4,600 m., that for the *Cladomania*-derived *Rigiocaulus* is 2,075-3 025 m. while that for the most ambiguous subgroup *Eusigmantha* is 3,001-3,700 m., a set which comes nicely in, and to be intermediate between, the two foregoing sets of figures. What is still more amazing is the same general proportion retained by the three "assemblages" of species within *Verticillatae* itself, the only important representative series of *Eusigmantha*. Herein, those species affiliated to *Nothosigmantha* as *P. rupicola* Franch., *P. Roylei* Maxim., *P. nana* C. E. C. Fisch. and *P. likiangensis* Franch. retain the highest figures; those akin to *Rigiocaulus* as *P. verticillata* L., *P. tangutica* Bonati, *P. refracta* Maxim. and *P. spicata* Pall. exhibit the lowest figures while those intermediate forms as *P. szetschuanica* Maxim., *P. diffusa* Prain, *P. involucrata* Tsoong and *P. lineata* Franch. show figures in moderate values.

Based upon the phylogentic relationships deduced from comparative morphology, our new system will have its most extraordinary, not improbably unique, feature in its convergent nature which coincides with the peculiarity in the evolution of the genus, and our systematic arrangement will also have the sharp cleavage at ends represented by the original groups, *Rhizophyllum* and *Sceptrum*, and all other derivative groups coming inbetween them. From the above statistics, our readers will not fail to see how close and thorough is the correlations maintained in the nature of the altitudinal dispersions revealed under various groups and subgroups in the genus to the unusual feature of our system. And such correlations exist not merely on subdivisional level, within the genus as a whole, but likewise on still lower levels as the subgroups within a group and even the three "assemblages" of species within a single series like *Verticillatae*. The revelation of the hidden connections between tolerance and phylogenetic ties by altitudinal distribution is truly remarkable.

The value of vertical distribution has been used here positively to give proof to the phyletic nature in the arrangement of our system, but it can just as well be utilized to detect any systematic flaw. For instance, *P. salicifolia* Bonati and *P. integrifolia* Hk. f. have been united to form a section, *Holophyllum*, by Dr. Li on their superficial resemblance. In our table, the elevation value for the former (to be found under Group *Sigmantha*, subgroup *Rigiocaulus*) is 900—3,500 m.[1] and that for the latter (to be found under group *Brachyphyllum*, subgroup *Eubrachyphyllum*) is 2,700-4,200 m. Besides the reasons from morphological view-point[2], we have also sufficient justification to regard these two species as phylogenetically distant on the very ground of the altitudinal differences. It will be seen that the disharmony in their figures when arbitrarily kept together dissappears as soon as they are severed and kept respectively into *Rigiocaulus* and *Eubrachyphyllum*. The same condition prevails also in the positions allocated to ser. *Muscicolae* and *Longiflorae* in Dr. Li's system.

Besides the afore-stated, some other points of interest are revealed in our study in the altitudinal distribution of *Pedicularis*. Firstly, it is demonstrable that allied species usually grow in similar elevations, but changes in the partiality to elevation are of common occurence; also that such changes occur usually in a gradual manner, and once started, it takes, as a rule, a definite direction without much oscillation,

1) The upper limit in this set of figures seems to be somewhat too high. Just as the altitudinal records for other species in the table, it may be quite inaccurate. But there is no other way than to take it as it is.

2) See observation under subgroup *Rigiocaulus* in the systematic treatment.

either upwards or downwards, until a limitation, controlled probably by the collective tolerance of the unit, is reached, when there may ensue another change in the opposite direction. Because of such slow changes, species occupying remote positions in the evolutionary procession of a unit may inhabit far distanced elevations. Secondly, species which maintain broader ranges of elevation are, generally speaking, also those that retain at once more wide areas geographically, as examplified by *P. Oederi* Vahl, *P. longiflora* Rudolph etc. Inside *Eucyclocladus*, it is *P. gracilis* Wall. (1,800-3,900. m) that solely ranges from Yunnan to Afghan. This correlation is evidently due to greater amplitude in the tolerance of these species.

Lastly, it is worthy to note here that any service the altitudinal data can render us would only come under the condition that they be studied in association with the system under phylogentic view-point[1]. Free grouping of species proximate in elevations tell us very little, and this is most clearly indicated by the case in *Rhizophyllum* and *Sceptrum*. By the descent of the former and the ascent of the latter, it is inevitable that sooner or later, the members of these opposing units would come to meet at certain elevations. There is thus difficulty in appreciating an enumeration in which species are kept together simply on the ground that they grow together at same elevations. (to be continued)

1) It would be interesting to compare my view in this topic with the view expressed by Van Steenis ("On the origin of the Malaysian mountain flora", a literature unavailable here at present), and referred to by Cain (l.c. 269) in relation to "Vicarious forms and areas". Our study has shown in no uncertain terms that comparison in the altitudinal differences between species can be quite instructive, although the results depend wholly upon the propriety of relationship between the species compared. To match species without closest affinity yield scarcely anything of value, it is true, but it does not necessarily mean that all such comparisons are entirely meaningless.